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XXXIV.

GALATHEA

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L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY

R. J. DANIEL, D.Sc.

XXXIV.

GALATHEA

BY

RICHARD B. PIKE, Ph.D.

DEPARTMENT OF ZOOLOGY, UNIVERSITY, READING

(With 20 Plates)

THE UNIVERSITY PRESS OF LIVERPOOL

FEBRUARY, 1947

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EDITOR'S PREFACE

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the fauna and flora of the Irish Sea.

Dredging, trawling and other expeditions, originally organised by the Committee, have been carried on intermittently since that time, and a considerable amount of material has been accumulated.

Five volumes on the fauna and flora of Liverpool Bay have been issued and a Manx Marine Fauna List was published in 1937. The latter contains complete data with regard to the distribution and breeding of all marine animals recorded from waters about the Isle of Man, except the seals and Cetacea. In this List past records, commencing with those of Edward Forbes, have been brought up to date, and new additions have been made as a result of intensive study of the shore fauna by members of the Port Erin Biological Station staff, with the collaboration of visiting biologists.

The papers in the present series, started in 1899, are quite different from the publications mentioned above, in name, in treatment and in purpose. Each Memoir treats of one type and is issued separately when ready.

Under the guidance of the late Sir William Herdman, the founder of the series, the Memoirs assumed a definite format and character, and they became well known as aids to the study of British marine animals and plants.

Consequently, when the Liverpool Marine Biology Committee ceased to exist and publication was transferred to the Oceanography Department, University of Liverpool in 1920, the name "L.M.B.C. Memoirs" was retained.

The forms selected are, as far as possible, common Irish Sea animals and plants of which no adequate account already exists in the text-books.

We are indebted to the ROYAL SOCIETY for a grant towards the publication of the present Memoir *Galathea*.

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PREFACE

THE greater part of the work for this memoir was done in the Zoology Department of Reading University and formed the basis of a thesis for the degree of Ph.D. of that University. It has been completed while a member of the staff of the Marine Station, Millport. I am deeply indebted to Reading University for their financial help during that time and especially to Professor C. H. O'Donoghue for his guidance and ungrudging help at every stage of the work. I am grateful to Professor F. J. Cole, F.R.S., under whom I took my Bachelor of Science Degree, whose encouragement and advice have been most stimulating ; to the late Dr. S. Kemp, F.R.S., and the staff of the Marine Biological Association at Plymouth for their kindness and interest on my frequent visits to the Station. I am especially indebted to Professor C. M. Yonge, F.R.S., of the University of Glasgow, for the care he has taken in checking some sections of the work. I also wish to acknowledge the helpful interest which I have unfailingly received from the Director of this Station, Mr. R. Elmhirst. Lastly, in great measure I owe the privilege of being able to produce this memoir to Professor F. Balfour-Browne, late of the Imperial College, who has been my mentor constantly from the start.

RICHARD B. PIKE

The Marine Station,
Keppel Pier,
Millport,
Buteshire.

L.M.B.C. MEMOIRS

No. XXXIV. GALATHEA

BY

RICHARD B. PIKE, PH.D.

University of Reading

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INTRODUCTION

In the super-family Galatheidea (Henderson, 1888) there are about 450 species, while in the family Galatheidae there are some 230 species. *Galathea* is a genus with a world-wide distribution, but precise information concerning its habitat-range is not yet available.

In Great Britain there are five species, all of which are similar in appearance, two species, *G. nexa* and *G. dispersa*, being so alike as to have caused confusion for some time. There should now, however, be no difficulty in separating those species in the British fauna by the key produced by Bull (25), which is given on page 5.

The species *Galathea squamifera* has been chosen for a morphological study because it is one of the least modified members of the Anomura. It also has the advantage of being easily procurable, but unfortunately is difficult to keep for any length of time under artificial conditions.

Description of distinctive points is given in full, but is reduced to a minimum where the anatomy of *Galathea* differs but slightly from that of other Decapoda. At the end of each anatomical section a comparison is attempted between *Galathea* and the other decapods. It has been found impossible in the time available to cover the literature fully and there are bound to be important omissions and many errors for which apologies are offered. It is hoped, however, that in spite of these shortcomings, the work will stimulate further study on the inter-relationships of the Decapoda.

CLASSIFICATION

Linnaeus (79) was the first to notice *Galathea strigosa*, and called it *Cancer strigosus* in 1761. Fabricius, in 1793, erected the genus *Galathea*, of which *G. strigosa* Linné is the type species.

The next use of the name *Galathea* was by Lamarck in 1805 (71), who applied it to a Lamellibranch. The name used by Fabricius therefore has priority over that of Lamarck.

The authors responsible for naming the other four British species were :—

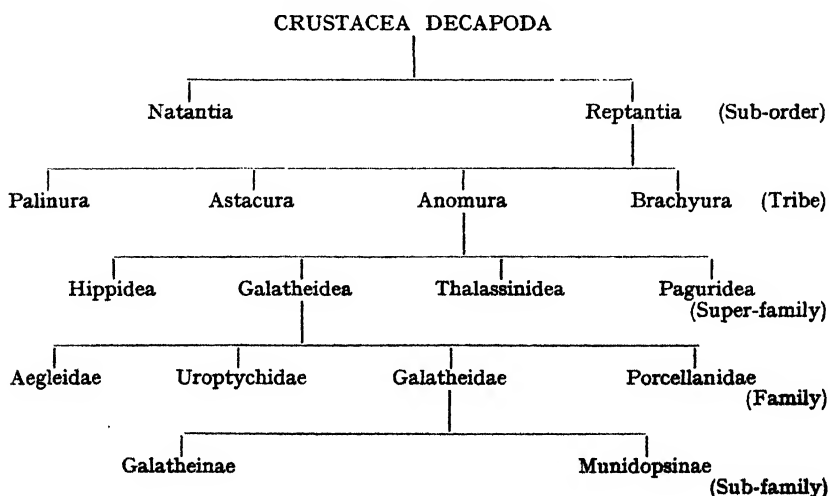
| | | | |
|----------------------------|-----|-----|------------------------|
| <i>Galathea squamifera</i> | ... | ... | Leach, 1814 (73). |
| <i>Galathea nexa</i> | ... | ... | Embleton, 1836 (38). |
| <i>Galathea intermedia</i> | ... | ... | Lilljeborg, 1851 (78). |
| <i>Galathea dispersa</i> | ... | ... | Bate, 1859 (6). |

For *Galathea nexa* Sherborn (115) gives the date for Embleton's paper as 1836, whereas H. O. Bull (25) says that the paper was first published in 1834. Mr. J. R. Le B. Tomlin has kindly looked up this paper in the British Museum and confirms the date given by Sherborn.

According to Englemann (39) the date of Bate's paper is 1858, and Bull gives the date as 1859. The Librarian of the Linnean Society kindly informs me that the paper was published in 1858, although the title-page bears the date 1859. Volume 3 consists of numbers 9-12. The first two numbers were published in 1858, and the last two in 1859. The paper in question occurs in number 9.

The classification here adopted is that put forward by Borradaile (15, 16), from which the following table has been taken, and a key to the British species of *Galathea* is also included from the work of Bull (25).

Borradaile's classification of the decapod Crustacea.



Key to the British species of *Galathea* :—

1. Basal joint of antennule with two strong spinous processes *G. intermedia*
 Basal joint of antennules with three strong spinous processes 2
2. Propodus of chelipeds with spines on dorsal surface ;
 pereopods 1-5 without epipodites ... *G. strigosa*
 Propodus of chelipeds without spines on the dorsal
 surface ; epipodites on pereopods 1-3 3
3. Merus of third maxillipeds much longer than ischium ;
 the chelipeds covered with scaly tubercles
G. squamifera
 Merus of third maxillipeds of almost same length as
 ischium, or slightly shorter ; the chelipeds covered
 with setae, or with scales fringed anteriorly with fine
 setae 4
4. Abdominal segments with single transverse furrow ;
 chelipeds "furry" ; rostrum clear-cut and concave
 almost free from setae ; when living or dried, with blue
 labrum, and blue line on pleural fold ... *G. nexa*
 Abdominal segments with three transverse furrows ;
 chelipeds not "furry" ; rostrum almost straight and
 thickly covered with scales and setae ; no blue labrum
 or blue on the pleural folds *G. dispersa*

PART I

EXTERNAL ANATOMY OF *GALATHEA SQUAMIFERA*

EXTERNAL CHARACTERS

From the dorsal side it is obvious that *Galathea* can be divided into three regions or tagmata, a cephalothorax, an abdomen and a tail.

The abdomen is chosen to begin the description of *Galathea*, because in the abdomen certain basic features are present which require description before further examination of external characters can be made.

Abdomen (Plate I, II, Figs. 1, 2, 3, 5, 7, 9, 13. Plate III, Fig. 17)

The Abdomen consists of six somites or segments and the telson or tail. The telson is a median portion, not a segment, and is flanked by the much expanded appendages of the last abdominal segment, the uropods.

A cross section of an abdominal somite (Fig. 17) shows that there is a thick calcified exoskeleton covering the dorsal and lateral surfaces. The dorsal wall consists of a median plate, the *Tergum* (Figs. 13, 17, *terg.*), which is continued laterally into two folds whose dorsal surfaces are known as *Pleura* (Fig. 17, *pl.*) and ventral surfaces as *Epimera* (Fig. 17, *ep.*). The median ventral plate is known as the *Sternum* (Fig. 17, *s.*). This arrangement, with minor modifications, is repeated in each of the six abdominal somites.

Each tergum overlaps its posterior neighbour like the tiles on a roof (Fig. 13), and adjoining terga are connected by a chitinous membrane, the *Arthrodial Membrane*.

The tergum of the first abdominal somite (Figs. 3, 5, 7, 9, *terg.*) is almost entirely covered by the posterior edge of the carapace (*vide* page 8), and the rudimentary pleuron of each side is situated in an almost dorso-lateral position between the carapace and the second abdominal somite (Figs. 3, 5, 7, 9, *pl. 1*).

The remaining abdominal terga and pleura occupy more normal positions, with transverse grooves extending from one side to the

other. In *G. nexa* (Fig. 5) there is only one transverse groove, while *G. squamifera* (Fig. 3) and *G. dispersa* (Fig. 7) both have a strong central groove and a weaker one in front and behind it.

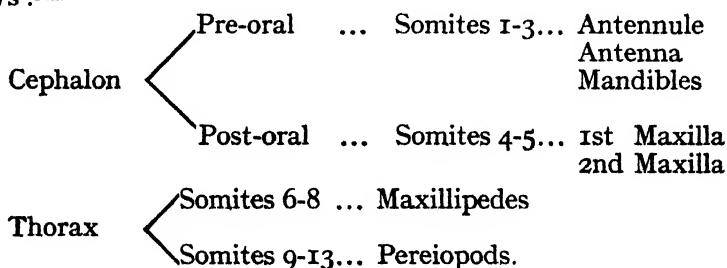
The description of the secondary sexual characters of the pleura and telson will be found on page 27.

The abdominal sternum is formed into a complete rod-shaped strut in the first somite only in the female. In the male this is extended to the second somite, probably due to the extra support required by the second pleopod (*vide* page 24), during copulation. In the female this rod is reduced to two calcareous centres (Plate I, Fig. 2). The remaining sterna are incomplete and similar for both sexes, being progressively reduced and becoming completely absent in the sixth abdominal somite.

When the animal is in a position of rest the abdomen is flexed beneath the thorax, but it is not held there by a locking arrangement as is found in the crab, since *Galathea* uses its tail for rapid backward propulsion.

Cephalothorax

The cephalothorax is so completely fused dorsally and laterally as to leave no signs of segmentation externally. The presence of 13 pairs of appendages on the ventral side indicates that the cephalothorax is composed of 13 appendage-bearing segments as follows :—



Embryological studies suggest the presence of an evanescent somite anterior to the antennules, and some authorities regard the eyes with their stalks as being the appendages of this somite. This is a matter of dispute and for the purposes of description the eye and its stalk will not be regarded as an appendage, nor will the evanescent somite, which does not show in the adult,

be taken into account. The antennular somite will be regarded as the first, but it is clear that if the other interpretation be accepted it is only necessary to add one to the number of the somite here employed.

In view of the developmental history of Crustacea, Goodrich (48) regards the mandibles as being post-oral. For *Cancer* Parson (99) represents the pre-oral epistoma (*vide* page 10) as forming the united second (antennary) and third (mandibular) somites. In the present work Pearson's view has been adopted.

The Cephalothoracic shield or Carapace (Plate II, Figs. 3, 5, 7, 9) is formed by the fusion of the terga and pleura of the segments of the head and thorax. It is divided into areas by means of depressions and grooves, and each area is named after the organ lying immediately below it. The lateral border of the carapace is armed with a number of sharp forwardly-curving teeth, known as the lateral teeth.

The Cervical groove (Figs. 3, 5, 7, 9, cg.) or branchial groove of Bouvier is the most prominent transverse groove and is situated about midway along the carapace. There does not appear to be any very reliable ground for maintaining that the cervical groove separates the cephalic region from the thoracic region, but it will be taken as doing so for purposes of description. The homologies of the terms by which writers have described the grooves dividing the carapace into areas are also not clear, and the following account is largely based on Borradaile (15, 16).

The cephalic portion of the carapace is divided into the facial, gastric and hepatic regions (Figs. 3, 5, 7).

The Facial region (Figs. 3, 5, 7, fr.) is separated from the remainder of the cephalon by a strong transverse groove, and is divided into a median region bearing the rostrum and two lateral orbital subregions.

The Rostrum (Figs. 3-8) is a depressed median prolongation of the carapace. It is flattened dorsoventrally and bordered laterally with spines in all British species of *Galathea*. The lengths relative to the carapace vary between these species. In *G. nexa* (Fig. 5) the length is shorter relative to the carapace than in

G. dispersa (Fig. 7), which presents an untidy appearance and appears almost straight as the spines are flatter and less sharp than in *G. nexa*. The rostrum in *G. squamifera* (Figs. 3, 4) is much broader than in *G. dispersa* (Figs. 7, 8) and has a more pronounced downward bend.

Immediately behind the rostrum lies the Gastric region (Figs. 3, 5, 7, 9, gr.), which is bounded on each side by a groove passing obliquely forward from the cervical groove. Bouvier called this groove the *linea anomurica* and Boas *line b*. The space between the *linea anomurica* and the cervical groove is the Hepatic region (Figs. 3, 5, 7, hr.).

The Thoracic region (Figs. 5, 7, tr.) is the whole area posterior to the cervical groove, and is not distinctly divided into areas. The cardiac region, clearly shown in most decapods, is only faintly marked off in some specimens of *Galathea*, while in other specimens the area is not delineated. The most prominent feature of this region is three strong transverse grooves, the hinder margin of the carapace is only slightly thickened.

All grooves of the carapace are bordered with simple uni-pinnate setae (Fig. 10), which are directed forwards, and the setae are closely set so that the pinnae overlap forming a close mesh.

Below the lateral teeth, the carapace bends ventrally through an angle of 90°, to form the Branchiostegite. This, when viewed from the side, is seen to be divided into two by the flexible Pleural suture (Fig. 9, pl. s.). The area ventral to the suture is known as the Pterygostomial region (Figs. 9, 12, pt. r.), and it projects forward at the sides of the epistome. In the notch between this and the forward continuation of the pleural fold is the antenna (Fig. 9, ant.). The pterygostomial region of *G. nexa* bears three bright blue marks (Fig. 12, shown in black). This colour is diagnostic for the species, and although retained in dried specimens is absent from those preserved in alcohol.

A series of long setae (Fig. 11) borders the anterior and ventral edges of the pterygostomial region. These setae in *G. squamifera* are simple, with fine irregular lateral branches, but are more complex in *G. intermedia* and *G. strigosa*.

Cephalothoracic Sterna

Unlike the carapace (terga and pleura) the sterna are not so completely fused and consequently a segmentation is indicated. This is made clearer, in spite of a certain amount of fusion of the sterna, by the fact that each segment (somite) has its own pair of appendages.

PRE-ORAL CEPHALOTHORACIC STERNA (Plate I, Fig. 2 ; Plate III, Figs. 14, 16) separate the articular cavities of the first two appendages, and form the anterior border of the mouth cavity (somite 3).

Sternum 1 (Figs. 14, 16, s1) separates the articular cavities of the antennules. Seen from the dorsal side these articular cavities are surrounded by thick rims and the sternum forms a bridge between them.

Sternum 2 and 3 (Figs. 14, 16, s2, s3) are fused together into a plate called the epistoma, which lies immediately posterior to the antennule (somite 1) and separates the articular cavities of the antennae (somite 2). The posterior margin of the epistoma forms a curved rim which is the anterior border of the mouth (somite 3). It therefore represents in part the united antennal and mandibular sterna s2, s3.

POST-ORAL CEPHALOTHORACIC STERNA (Plate III, Figs. 14, 16) form the posterior margins of the mouth cavity and the first and second maxillae.

Sternum 4 (Figs. 14, 16, s4) forms an incomplete sternal bridge which separates the articular cavities of the first maxillae and lies immediately posterior to the mouth.

Sternum 5 (Figs. 14, 16, s5) forms a complete sternal bridge which separates the articular cavities of the second maxillae and when viewed from the side it delimits the head region. The head, or cephalon, is therefore clearly marked off from the thoracic region (Fig. 15, s5) and weakly connected to it.

THORACIC STERNA (Plate I, Fig. 2 ; Plate III, Figs. 14, 15) are for descriptive convenience again split into the sterna separating :—

- (a) Maxillipedes.
- (b) Pereiopods.

The sterna separating the articular cavities of the maxillipedes fall in steps to the level of the thoracic cavity, and are best seen from the internal dorsal side (Fig. 14, s6, s7, s8).

Sternum 6 (Fig. 14, s6) is very reduced and occupies the most anterior dorsal position separating the first maxillipedes.

Sternum 7 (Fig. 14, s7) occupies a central position and is connected to the sternum eight by two stout supports. These are probably endosternal in origin (Fig. 14, e.st. 8).

Sternum 8 (Fig. 14, s8) forms the apex of the triangular plate separating the pereopods.

Sterna 9-13 (Fig. 14, s9-s13) are those separating the pereopods. They form a broad triangular plate divided by transverse grooves which mark the positions of the endosternal ingrowths. The 10th, 11th and 12th have also longitudinal median grooves which mark the positions for the ingrowth of the median plates (Fig. 15, md. pl. 10, 11, 12).

The fifth thoracic sternum is separated from the fourth thoracic sternum by an arthrodial membrane.

In the Brachyura the posterior corner of each sternum is divided by a suture to form the episternum. This suture is not present in *Galathea*, but as in the crabs the episternal area has a concavity for the articulation of the ventral hinge of the coxa.

Epimera.

CEPHALIC EPIMERA (Plate III, Figs. 14, 15, ep. 4, 5) are difficult to identify and for *Cancer* Pearson (99) thinks that they may be represented by the region between the outer portion of the articular cavities of these somites, while the epimera of the mandibles are probably represented by the membranous roof of the pre-branchial chamber at each side of the mandibles (Fig. 14, r. br.).

Two supports arise from somites 4, 5, and unite to form a bridge weakly interlaced in the mid-line (Figs. 14, 15, ep. 4, 5). These may be endosternal or epimeral in origin. They are here regarded as epimeral as a similar support in crabs appears to be epimeral.

THORACIC EPIMERA (Plate III, Figs. 14, 15, ep. 6-12) are represented by a continuous plate forming the inner wall of the

branchial chamber. They slope upwards and inwards from the pereopods, and are continuous above with the membranous roof of the branchial chamber. These fused thoracic epimera are divided transversely by sutures which mark the positions of endopleural downgrowths. The last thoracic somite has no epimera.

THE ENDOPHRAGMAL SYSTEM

The endophragmal system (Text-Fig. 1, Plate III, Figs. 14, 16) of the cephalothorax is made up of a complicated internal arrangement of plates used for muscle attachment and visceral support. Each sternal and epimeral transverse groove separating two somites marks the position of an infolding of the arthrodial membrane, which gives rise to a transverse series of incomplete double-walled partitions. One wall belongs to the somite in front and the other to the somite behind. The infolding from the sternal wall is called an *endosternite* and that from the epimeron an *endopleurite*.

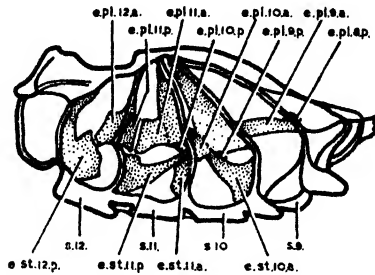
The sternal partitions are incomplete in the mid-line, as the endosternites arise only from the lateral margins of the sutures (Fig. 14), leaving sterna 10, 11 and 12 divided only longitudinally by three low median partitions called *median plates* (Figs. 14, 15, md.pl. 10, 11, 12). The endosternites between 9 and 10, 10 and 11, 11 and 12, grow upwards and inwards, interlocking to form a strong bridge under which the ventral nervous system passes (Fig. 14).

Each endopleurite gives off two laminae, one of which passes forwards to join the endosternite in front, while the other passes backwards to join the endosternite behind.

This is shown in Text-Fig. 1, where each anterior endopleurite passes backwards and is joined by the posterior endopleurite of the same somite before joining that posterior endosternite. This is most clearly shown in somite 11.

This simple state becomes modified and more difficult to appreciate anteriorly, owing to the increased backward slope of the epimeral sutures, and the large space required for the muscles of the chela. This causes the large endopleurite between

somites 9 and 10 to overshadow that between 10 and 11, and also reduces the size of the anterior endopleurite 10a (Text-Fig. 1, e.pl. 10a). The endopleurite arising between epimera 8 and 9 is



TEXT-FIG. 1

The epimera are removed to show the endophragmal system, lateral view right hand side. $\times 6$.

e.pl., endopleurites 8-12, a.anterior, p.posterior; e.st., endosternites 10-12, a.anterior, p.posterior; s., sterna 9-12.

modified into a strong strut which passes backwards to reinforce the thoracic bridge (Text-Fig. 1 and Fig. 14, e.pl. 9a), while the posterior endopleural plate of the 8th somite is reduced to a small lamina (Text-Fig. 1 and Fig. 14, e.pl. 8p).

The anterior thoracic endosternal and endopleural supports are exceedingly reduced and difficult to follow; the apparent positions of these are shown in Fig. 14.

The endophragmal system of *Galathea* occupies an intermediate position between that of *Homarus* and *Cancer*, and combines features of both. It does not consist as in *Homarus* of a transverse series of endosternites and endopleurites forming a sternal arch over the sternal sinus. There is only one strong arch in *Galathea* spanning the sternal sinus, a part of which must be reabsorbed during ecdysis for the extraction of the ventral nerve cord.

Galathea resembles *Cancer* in the reduction of anterior supports, and the spaciousness of the thoracic cavity with the backward slope of the epimera. The thoracic endosternites are more reduced than in *Cancer*, while the endopleurites basically resemble those of the Crayfish, as illustrated by Huxley (65).

APPENDAGES

There are five pairs of appendages on the head, eight pairs on the thorax, and on the abdomen the male has five and the female four pairs.

The terms used are those proposed by Hansen (55), and a short account of his terminology is given below.

The long terms endopodite, exopodite, and epipodite have been cut down to endopod, exopod and epipod. The name protopodite used for the proximal unbranched portion of the appendage has been replaced by the term sympod. A typical sympod has three segments: praecoxa, coxa and basis. To the distal joint of the sympod both the endopod and the exopod, if existing, are attached, giving to the typical biramous appendage a basal sympod and a distal endopod and exopod. Instead of the older names for the joints in the legs of Decapoda, viz., coxopodite, basipodite, ischiopodite, etc., the terms coxa, basis, ischium, merus, carpus, propodus and dactylus have been substituted.

Cephalothoracic Appendages.

THE ANTENNULE, somite 1 (Plate IV, Fig. 18) is situated below the rostrum, and slightly mesial to the eye (Fig. 2, 9). The basal joint is large and has three strong spinous processes whereas in *G. intermedia* there are only two.

The largest of these spines is lateral, and between the central and mesial spines a segmented appendage arises, the first two segments of which together with the spinous base form the sympod. From the distal end of the sympod arise two short but many-jointed processes. The larger is the exopod (Fig. 18, ex.), which bears a thick mass of setae on its ventral side. The smaller is the endopod (Fig. 18, end.), from which only a few setae arise.

Lying on the dorsal surface of the basal joint of the sympod is a small scale (Fig. 18, sc.), partly overlying a crescent-shaped slit, which is further protected by plumose setae. This marks the opening of the statocyst.

THE ANTENNA, somite 2 (Plate IV, Fig. 19) lies lateral to the antennule, and consists of a large basal coxa (Fig. 19, c.), which, on

its ventral side, is flat with a thickened border, and is distally perforated by the aperture for the duct of the antennary gland (Fig. 19, ap.g.g.). Above this aperture and lateral to it is a large spine.

Articulating with the coxa (Fig. 19, c.) is the basis (Fig. 19, b.), which has a short spine (Fig. 19, sp.) on the antero-mesial border at right angles to the joint. In *G. squamifera*, like *G. dispersa*, this spine is not more than half the length of the succeeding distal joint, whereas in *G. nexa* the spine is equal in length to that joint. On the antero-lateral border of the basis (Fig. 19, b.) there is another forwardly directed spine, which is also present in *G. nexa* and *G. dispersa*. On the dorso-lateral surface of the basis is a small movable scale which probably represents a reduced squame or exopod.

The flagellum (Fig. 19, fgl.), with its two large basal joints, represents the endopod (Fig. 19, end.). On the antero-mesial border of the basal joint of the endopod is a small spine present also in *G. nexa*, but absent in *G. dispersa*.

THE MANDIBLES, somite 3 (Plate IV, Figs. 20, 25), may be represented by the coxa, Borrodaile (15). They are strongly calcified, and provided ventrally with smooth sharp incisor processes (Figs. 20, 22, inc. pr.), which are separated from the dorso-ventral concave molar processes (Fig. 22, mol. pr.) by a deep groove. Into this groove fits the labrum which occupies a median position. The mandibular palps also work in this groove ventral to the labrum.

The mandibular axis of articulation is oblique, and the movement is towards and away from the middle line. The anterior articulating surface is on the dorso-lateral edge (Figs. 21, 22, art.) and the posterior angle articulates with the fourth sternum (Fig. 20, s. 4).

Extending into the body cavity from the base of the mandibles, and lying on each side of the cardiac portion of the gastric mill is an apophysis (Fig. 21, apoph.), at the distal end of which is a broad tendon for the attachment of the external adductor muscle (Fig. 21, t. ex. ad.). On the medial edge is a long thin tendon which extends to the gastric region of the carapace (Plate II,

Fig. 3) and to which the internal adductor muscle (Fig. 21, t. int. ad.) is attached.

The mandibular palps (Figs. 20, 21, md. palp., and Figs. 23-25) arise from the antero-lateral border of the mandibles, and are three-jointed. The terminal joint is foot-shaped with a not very pronounced heel (Figs. 21, 23-25). This is more pronounced in *G. nexa* (Fig. 25) than in *G. squamifera* (Figs. 21, 23) or *G. dispersa* (Fig. 24). There are setae along the anterior edge and apex in all three species, but *G. dispersa* has a few plumose setae (Fig. 24, pl. hr.) on the proximal ventral edge, which are not found in *G. squamifera* or *G. nexa*. The basal joint in all three species has an oblique row of setae.

In *G. squamifera*, as already mentioned, the terminal joint of the mandibular palps works in the concave dorsal portion of the mandibles, and helps to retain the food in the oesophagus.

The mouth lies dorsal to the mandibles and is bordered laterally and ventrally by the metastoma (Fig. 20, met.), which gives off fleshy lobes on each side; these cup the ventral surface of the mandibles.

THE FIRST MAXILLA, somite 4 (Plate V, Figs. 26-28) is a thin leaf-like appendage arising immediately ventral to the mandible. The sympod is composed of three joints: praecoxa, coxa and basis. There is no exopod and only a simple endopod (Fig. 26, end.).

The first joint of the sympod is the praecoxa (Fig. 26, pr.) which may consist of the short attachment base with its few long setae. The second joint is the coxa (Fig. 26, c.), a large somewhat rectangular plate with the mesial border fringed with stiff setae. Some of these setae form miniature forks and aid the passage of the food to the mouth. The whole lamina is prevented from swinging away from the body by its line of attachment and skeletal support (Fig. 27, skel.).

The lateral border of the coxa has a plate-like extension (Fig. 26, ext.) which is rudimentary in some types of Decapoda, but is especially well developed in *Gebia*, *Porcellana*, *Galathea*, *Munida* and *Dromia*. According to Hansen (55) this is the same plate that is found in the majority of Euphausiacea, and described by

him as the pseudexopod. This plate-like extension is usually referred to as an exite (Fig. 26, ext.).

The third joint of the sympod is the basis (Fig. 26, b.). It is spatulate, and the mesial border also has stout but simple setae.

THE SECOND MAXILLA, somite 5 (Plate V, Fig. 29) overlies the first maxilla, and is built on a similar plan except that the coxa and basis are bilobed. The endopod (Fig. 29, end.) is two-jointed, and the lateral plate has been greatly extended to form an exopod and scaphognathite.

The praecoxa (Fig. 29, pr.) forms a well chitinated joint separated from the bilobed coxa (Fig. 29, c.) by a deep suture. The basis (Fig. 29, b.) is also well delimited by sutures, and the mesial borders of both basis and coxa are fringed with simple setae.

The endopod (Fig. 29, end.) is still simple and made up of two joints, while the exopod (Fig. 29, ex.) is a large lamina occupying a lateral position. Both exopod and endopod appear to be attached to the basis.

Arising from the proximal end of the exopod is a triangular scaphognathite (Fig. 29, scap.), which has a skeletal stiffening. According to Calman (28) the scaphognathite must be regarded as an extreme development of the exopod.

THE FIRST MAXILLIPED, somite 6 (Plate V, Fig. 30) is slightly stouter, but has not taken on the general form of the thoracic limbs, and is little different from that of a maxilla.

The praecoxa (Fig. 30, pr.) is small, and the coxa (Fig. 30, c.) and basis (Fig. 30, b.) are both single lobed with simple setae on their mesial borders.

The endopod (Fig. 30, end.) is simpler than in the second maxilla, while the exopod (Fig. 30, ex.) has developed into a strong two-jointed appendage with the distal joint corresponding with the flagellum (Fig. 30, fgl.).

The lateral border is occupied by a thin laminated epipod. (Fig. 30, epi.).

THE SECOND MAXILLIPED, somite 7 (Plate V, Fig. 31) more nearly approaches the general type of thoracic limb than does the first maxilliped.

The endopod, although relatively short and permanently flexed towards the mesial line, has the seven typical joints of the ambulatory legs, i.e., coxa, basis, ischium, merus, carpus, propodus and dactylus. The first two joints form the sympod, and there is no epipod on the coxa.

The exopod (Fig. 30, ex.) has greatly developed and the flagellum (Fig. 30, fgl.) is again flexed towards the mesial line, with a terminal tuft of plumose setae.

According to Hansen (55) the ischium and merus in Decapoda must in some way be homologous with the three joints in the Peracarida, and he suggests the existence of a praeischium. A praeischium is more or less conspicuously marked off in some genera by an oblique transverse impression or suture, but in *Galathea* and *Munida* the praeischium is completely fused with the ischium.

THE THIRD MAXILLIPED, somite 8 (Plate V, Figs. 32-34) shows a slight reduction in the exopod (Fig. 32, ex.), with an increase in length and complexity in the endopod. The endopod (Fig. 32) is typical in having the seven joints of the ambulatory legs. The proximal joint bears the curved shaped epipod (Fig. 32, epi.), and the coxa (Fig. 32, c.) and basis (Fig. 32, b.) are connected by an immovable articulation. The ischium (Fig. 32, i.) shows no sign of a praeischium, and its mesial border is serrated. The lateral border of the merus (Figs. 32, 34) is fringed by a double row of long setae (Fig. 34), which do not show any special modifications, but the setae of the dactylus (Figs. 32, 33) are of the two kinds, simple and serrated. The serrated setae (Fig. 33) are sickle shaped and used for cleaning the cephalon.

A typical pereopod (Plate VI, Fig. 39), or ambulatory leg, consists of seven joints or podomeres. The two proximal joints constitute the sympod, and the five distal joints the endopod. These joints named from the base to the apex are as follows: (1) Coxa, c., (2) Basis, b., (3) Ischium, i., (4) Merus, m., (5) Carpus, c', (6) Propodus, p., (7) Dactylus, d. There is no exopod.

The basis and ischium are fused together, and at this junction

autotomy takes place. Pearson (99) calls the joints formed by this fusion in *Cancer* the basi-ischium, but this term appears unnecessary and will not be employed.

Herrick (63) points out that owing to the weakness of this junction in *Homarus* any lateral movement would be serious and liable to cause fracture. This is guarded against by the use of an interlocking spur on the basis, and it is only when the strain is sufficient to overcome this extra support that autotomy occurs. In *Galathea squamifera* there is a similar arrangement with a single large interlocking spur (Fig. 38, i. sp. 1) arising from the basis.

This is slightly overlapped laterally by another spur (Fig. 38, i. sp. 2) arising from the ischium. When any lateral backward strain takes place the ischium is levered against the spur (i. sp. 1), and if the strain is sufficient to overcome this support the ischium is forced out of the small ball and socket joint on the mesial side (Fig. 38, s. j.), and the leg parts along the fracture plane (Figs. 35, 36, 38, f. p.).

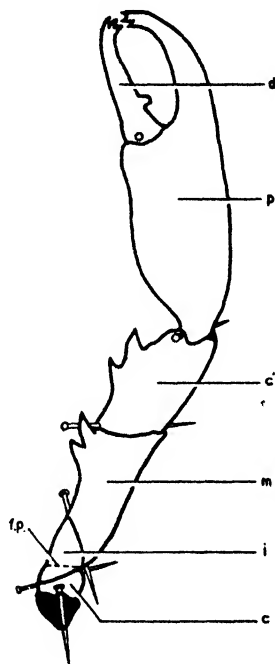
The coxa articulates with the sternum and the successive limb joints are articulated with one another by arthrodial membranes and usually also by hinges. The direction of movement is at right-angles to the axis of articulation or the line joining the hinges. As each axis is on a different plane the net result is almost that of a universal joint (Text-Fig. 2).

Herrick (63) points out that in the larval stage of *Homarus* the dactylus moves in a vertical plane, while in the adult it moves in a horizontal plane; a torsion of ninety degrees having taken place towards the mesial line. Most of this torsion takes place in the carpus, and is completely effected by the fourth larval stage. It seems that a similar torsion has taken place in *Galathea*.

In the sectional view of the first pereopod (Plate VI, Fig. 36), the tendons (t. fl. 1-6, and t. ex. 1-4) are shown. These tendons are derived from ingrowths, or flattened pockets in the arthrodial membrane. They are attached to the proximal end of each joint, and pass backwards into the joint proximal to it. The muscles attached to these tendons are of two kinds, flexor muscles

attached to tendons (t. fl. 1-6) flex those joints, while a contraction of the extensor muscles attached to tendons (t. ex. 1-4) on the opposite side returns the joints to their previous positions.

THE FIRST PEREIOPOD, or chela, somite 9 (Plate VI, 35-38) is usually a little longer than the body and possesses the seven podomeres of the typical walking leg, on the coxa of which is a small epipod (Fig. 35, epi.).



TEXT-FIG. 2

Outline of right chela with pins denoting the axis of articulation. $\times 2$
c., coxa; *i*, ischium; *m.*, merus; *f.p.*, fracture plane; *c'*, carpus; *p.*, propodus;
d., dactylus.

The mesial surface of the m e r u s and i s c h i u m (Fig. 35, m., i.) is covered with a felt of setae, while in *G. nexa* the whole appendage is setae. The distal mesial edge of the merus also bears three strong spines, while the lateral border is bounded only by small denticles. The c a r p u s (Fig. 35, c'.) is similar to the merus except that the setae are fewer and there are only two spines on the mesial border. In the seven specimens of *G. nexa*

examined there was only one prominent spine on the carpus, while *G. dispersa* has one prominent spine and a number of smaller ones. As Bull (25) did not mention this as being a specific character, it may be variable. In the propodus (Fig. 35, p.) and dactylus (Fig. 35, d.) the marginal spines of both sides have given way to denticles, and the whole surface is thickly covered with scale-like plates.

In young *Galathea squamifera* the dactylus makes contact along its whole length with a finger-like extension of the propodus. At the tip of both these joints are three sharp teeth which interlock and prevent lateral movement, and also aid in gripping the prey. Along the inner edges of the dactylus and the propodus extension are numerous tufts of tactile setae, and situated among these setae on both joints is a single row of small tubercles. They can hardly be called denticles and have little or no cutting power.

In the female the dactylus remains in close contact with the propodus throughout life, but in the male sexual differentiation takes place. The animal becomes right or left-handed by the enlargement of that hand, with an increased width of the propodus, and by the curvature of both propodus and dactylus. The forceps are now no longer in contact except at their apices (Fig. 35), a tubercle develops on the inner proximal edge of the dactylus (Fig. 35), and in some old specimens a corresponding tubercle meets it from the propodus. It appears that this male sexual differentiation is partly or completely lost at the autumn moult and regained on moulting in the spring.

It is difficult to see what benefit is derived from this displacement of surfaces, or from the growth of the tubercle. The sharp tips will certainly have a more offensive quality, and in many of the specimens collected the propodus bears puncture scars. The puncturing must have been done soon after ecdysis, as the hardened shell is too tough for penetration by another male during combat. It is also possible that the tubercle has some function during copulation.

An examination of the other British species shows that all males possess this right or left handedness, although it is not so pronounced in *G. strigosa*, nor does the examination of young

specimens reveal if they all begin right or left handed, and change over on the loss of a limb.

On measuring specimens it is found that the $\frac{\text{chela length}}{\text{body length}}$ remains fairly constant at 1 : 1, but the $\frac{\text{length of propodus}}{\text{width of propodus}}$ is considerably more for the male 1.4 : 1.

On the dorsal surface of the merus the calcified exoskeleton is interrupted by a narrow track of uncalcified chitin (Fig. 35, dotted track). This weakening may allow the constricted base to expand for the extraction of the limb during ecdysis.

The limb joints articulate by means of two condyles working in sockets (Fig. 37), and these are held in position by arthrodial membranes. There is no lock hinge as is described by Herrick (63) for *Homarus*.

THE SECOND PEREIOPOD, somite 10, is similar to the third and fourth pereopods.

THE THIRD PEREIOPOD (Plate VI, Figs. 39) is chosen for description. It is non-chelate and covered with scale-like plates fringed on the anterior margin with setae. The coxa (Fig. 39, c) bears a small epipod (Fig. 39, epi.), and the fracture plane is similar to that already described. The dactylus (Fig. 39, d.) is pear-shaped with a sharp apex, and is well supplied with tactile setae.

All the joints are loosely articulated, and the tendons for muscle attachment (Fig. 40) are similar to those described for the chela.

THE FIFTH PEREIOPOD, somite 13 (Plate VI, Figs. 41-43) is chelate and used for cleaning and not for walking. In life this folded appendage is closely applied to the body in a vertical position. It does not bear an epipod, but the coxa in the male does bear the external opening for the vas deferens (Fig. 41, vd.o.). The basis (Fig. 41, b.) is fused to the ischium (Fig. 41, i.), but there is no fracture plane. The propodus (Fig. 41, p.) and dactylus (Fig. 41, d.) bear a thick mat of setae, and Zimmerman (136) noticed that these were modified for cleansing purposes and rather implied that all the setae were

of the serrated type ; the serrated setae (Fig. 42) are in fact confined to a single broad band on the propodus. Zimmerman's drawing shows these setae as having only a single row of denticles, whereas the row is double (Fig. 43). The remaining setae are straight and only minutely serrated.

When the pereopod is moved by means of forceps, so that it is in a position to clean the grooves on the carapace, the curved hairs with the serrated edges are then pointing into the grooves.

The *dactylus* (Fig. 41, d.) is shaped like a duck's bill, and articulates against a correspondingly flat extension of the propodus. The axis of articulation is in the same plane as the curved setae, so that when brushing the carapace the lamellae of the "bill" are in a vertical position, and so are able to "preen" the setae of the carapace. Both edges of the "bill" have raised horny margins and short tactile setae. Zimmerman (136) did not mention the chelate nature of the limb, a characteristic so obvious that its oversight must have been one of description only.

On the opposite side of the propodus is a broad band of short setae probably used for brushing. The whole appendage is therefore well adapted as a cleaning organ, and is at times inserted into the branchial cavity for cleaning of the gills.

Abdominal Appendages (Plate VII, Figs. 44-52)

There are five pairs of abdominal appendages, or pleopods, in the male and four pairs in the female.

In the male these appendages can be divided into two groups. The first two pairs are modified to subserve the function of copulation, and the last three are alike and used as swimmerets.

In the female the first abdominal somite bears no appendage while the next four somites have pleopods modified for egg attachment. They differ from any of the male pleopods but are themselves similar, although the first appendage is only about half the size of the posterior three.

THE FIRST PLEOPOD of the male, somite 14 (Figs. 44-45, 47) is composed of a cylindrical basis (Figs. 44, 45, b.) to the distal end of which is attached the *endopod* (Figs. 44, 45, end.). The endopod takes the form of a partly rolled lamina, the distal

end of which has a series of long simple setae, while the inner border is edged with a series of short setae.

THE SECOND PLEOPOD of the male, somite 15 (Figs. 46, 47) has a two jointed sympod composed of a small *coxa* (Fig. 46, c.) and a cylindrical *basis* (Fig. 46, b.). Attached to the distal end of the basis is a small scale-like *exopod* (Fig. 46, ex.), and a grooved laminated *endopod* (Fig. 46, end.). The first and second pleopods fit together in life to form a complete tube for the conveyance of the spermatophores to the female pleopods, where they are attached prior to egg laying (*vide* page 116).

THE THIRD, FOURTH AND FIFTH PLEOPODS of the male, somites 16-18 (Fig. 48) are essentially similar to each other, the sympod being made up of a small *coxa* (Fig. 48, c.) and a much larger spatulate *basis* (Fig. 48, b.). The basis has from twenty to twenty-six plumose setae on its lateral border, each seta having a segmented central shaft with lateral pinnae. Each segment bears from five to seven paired pinnae (Fig. 49), and each pinna is a thin lamina shaped like a knife blade. The blade is composed of extremely thin chitin which is evident when stained with chlorazol black E. This description does not agree with that given by Pérez (103), but the point is of small moment.

Articulated with the mesial end of the basis is a two-jointed *endopod* (Fig. 48, end.). The spatulate basis with the two-jointed endopod is typical of the male, but it should be noted that young females possess typical male abdominal appendages until a size of from 11-15 mm. is reached, when an inter-sexual stage becomes evident before the true female limb is developed (*vide* page 25). In the inter-sexual stage (Fig. 51) it will be seen that the lamina of the basis is reduced (Fig. 51, b.) and the two-jointed endopod elongated. Long simple setae grow and eventually the whole appendage takes on the cylindrical female form. It is essential to appreciate this when interpreting the pleopods of those *Galathea* carrying parasitic *Epicarida* or *Rhizocephala*.

Deformities also occur, as in Fig. 50, where a second basis has been developed inverted at the distal end of the first.

THE FEMALE PLEOPODS (Fig. 52) are all of one type, the first arising from somite 15.

The first pleopod commences development as a short styliiform appendage, and may remain unformed for some time after the three posterior appendages have taken on the mature female form. According to Pérez (100), the setae of this limb when mature are scattered, and not well bunched as in the posterior three pleopods ; also there may be a few plumose setae among the simple setae. This with its post larval development appears to give to the limb a character in some way special to itself. The second, third and fourth female pleopods are alike (Fig. 52). They are cylindrical and have four joints bearing tufts of simple setae for egg attachment. At the spring moult (January-February) the length of these setae is considerably increased.

For the development of the posterior three pleopods refer to the male inter-sexual stages on the previous page and to Fig. 51.

THE UROPOD, or sixth abdominal appendage, somite 19 (Plate VII, Fig. 53) is similar in both the male and female and consists of two parts, a proximal roughly triangular sympod, to which are attached an exopod (Fig. 53, ex.) and an endopod (Fig. 53. end.), both of which are circular and plate-like.

The uropod is the only abdominal appendage with a fully formed exopod, the outer edge of which is finely denticulated, and has a fringe of plumose setae similar to those bordering the basis of the male pleopod. On the dorsal lamina are scattered groups of denticles arranged in transverse rows, each composed of from three to six teeth.

The endopod is similar to the exopod but more robust. The denticles on the dorsal surface are more pronounced and occasionally have a stiff seta between the outer pair of teeth. The groups of denticles are also mainly arranged in a longitudinal series and not scattered over the surface as on the exopod.

Pérez (101) notes that in the genus *Aeglea* the sexual differences are shown, not on the telson as in *Galathea*, but on the posterior edge of the basis of the uropod, and in the ornamentation of the external margin of the endopod of the same uropod. The male is

distinguished as in *Galathea* by a preponderance of acicular setae, while the female has only soft plumose setae.

THE TELSON (Plate VIII, Figs. 54-60) is similar in shape for both the male and female and is made up of a number of calcified plates connected by chitin. There is slight individual variation in the shape of the plates (Figs. 54-55), but the resemblance is always sufficiently close for generic and specific diagnosis. Pérez (191) in an excellent paper points out the significance of the telson as a specific character.

The telson articulates with the sixth abdominal somite by means of the Median Plate (Figs. 54, 55, med. pl.). The median plate is flanked on each side by the small triangular Anterolateral Plates (Figs. 54, 55, ant. ltr. pl.), to which the basis of the uropod is attached. Posterior to the anterolateral plates are the Lateral Plates (Figs. 54, 55, ltr. pl.). these are roughly triangular and show seasonal secondary sexual characters. The telson is terminated by the two Posterior Plates (Figs. 54, 55, post pl.) connected in the middle line by chitin. In the centre of the telson is a soft incompletely calcified area called the Central Plate (Figs. 54, 55, cent. pl.), while lying on each side of this area are two small triangular Intermediate Plates (Figs. 54, 55, int. pl.). The anus opens on the ventral side directly under the central plate.

Each plate has scale-like ornamentation. The posterior edges of these plates are bordered by plumose setae, among which are sometimes situated strong acicular setae. The ratio of plumose to acicular setae appears to be constant for a given species, and in conjunction with the plates forms a fairly reliable specific character.

Pérez (100) did not separate *G. nexa* from *G. dispersa*, as at the time of publication of his paper the specific differences were still debatable. The telsons of *G. nexa* (Fig. 56) and *G. dispersa* (Fig. 57) differ slightly but they may be separated by means of the setae bordering the scales of the posterior plates (Figs. 59, 60). In *G. nexa* (Fig. 59) there are usually two plumose setae on each side of a stout simple seta when this is present. The number of plumose setae may be increased to three on one side and two on the other, or reduced to one on each side. In *G. dispersa* (Fig. 60)

the number of plumose setae is usually four on each side, or three on one side and four on the other, but the number of setae in the specimens examined is always higher than that found in *G. nexa*. In *G. squamifera* (Fig. 58) there are often two non-plumose setae and always numerous plumose setae.

The shape of the central plate is variable, and cannot be used for separating *G. nexa* from *G. dispersa*, nor can the length to the breadth ratio of the telson be used.

SECONDARY SEXUAL CHARACTERS

Seasonal Secondary Sexual Characters of the Telson (Plate VIII, Figs. 54-57) allow for easy separation of the sexes, although this is not so obvious as the form of the pleopods. The most conspicuous sexual character is to be found on the free border of the lateral plates of the telson (Figs. 54-57, ltr. pl.). Along this border in the male *Galathea* are grouped strong yellow sabre-shaped acicular setae, with their ends curved towards the rear. On the anterior half of the border of the lateral plate these setae are arranged in four or five ranks, which become a single row in the posterior half. In the female the external margin of the lateral plate (Fig. 55, ltr. pl.) has a few acicular setae on its anterior portion but these are soon replaced by plumose setae. After the September-October moult the male sexual characteristics of the telson are lost (*vide* page 33), the characteristics being regained at the January-February moult.

The male sexual characters are not noticeable until the animal is 8-10 months old (*vide* page 118).

Seasonal Secondary Sexual Characters of the Pleura (Figs. 61-64) are to be found on the ventral surface of the pleura, where plumose setae are situated just inside the apparent margin, and so really belong to the epimera. The first abdominal segment is rudimentary and shows nothing of importance. The second abdominal pleuron (Figs. 61, 62) is the first to occupy a normal position, and shows sexually distinct characters in the arrangement of the plumose setae. In the male the plumose setae are short and arranged in a single irregular row,

indicated by the attachment scars (Fig. 61, att. scr.). In the female the setae are three times as long as those of the male, and the number of rows is increased to five or six. This forms a broad band in front tapering posteriorly to two rows (Fig. 62, att. scr.).

The plumose setae on the third, fourth and fifth abdominal pleura differ from those on the second, but are themselves alike in the same sex. The fifth abdominal somite has been chosen for description (Figs. 63, 64). In the male (Fig. 63) the anterior edge of the pleuron has a series of small plumose setae. These setae become noticeably longer towards the posterior edge, leave the external margin and become attached to the underside at the junction of the epimeron. In the female (Fig. 64), the plumose setae commence as in the male, and leave the margin at about the same place, but they are three times as long as those of the male and are arranged in two ranks.

The sixth abdominal pleuron, which bears the uropods, is sharply triangular and bears on its anterior and posterior edges a border of plumose setae. The females have a few more setae, which are again three times as long as those of the male.

After the September-October moult these characters are lost and the setae return to a condition approaching that of the male, but are regained at the January-February moult.

As in the male telson the female sexual characters of the pleura are not noticeable until the animal is 8-10 months old (*vide* page 118).

Further details on these secondary sexual characters will be found in the excellent papers by Pérez (100, 101, 102). He did not, however, notice that the above arrangement was seasonal.

The agent affecting these changes is not known but evidence would tend to indicate the presence of a sex hormone.

Sexual Dimorphism in other Galatheidæ

Pérez (101) has examined the range of forms exhibited by the entire family, and put forward some interesting generalisations.

It seems that secondary sexual characters appear throughout the Galatheidæ, and in this respect the following genera are

closely analogous with *Galathea* : *Pleuionoedes*, *Grimothea*, *Galaecantha*, *Munidopsis*, *Galathodes* and *Elasmonotus*. In these genera the lateral plate of the telson is furnished throughout the extent of its free margin with a comb of stiff setae similar to those already described for *Galathea*. In the female the same margin bears plumose setae, or is without ornamentation. It is strange that in this series the genus *Munida* stands alone as an exception, for the majority of its species show no secondary sexual characters on the telson. They are present, however, to some extent in *M. iris*.

In *Eumunida*, *Gastroptychus* and *Diptychus*, where the caudal fan is reflexed under the abdomen, no sexual differences are exhibited, and in the genus *Aeglea*, which is the only representative of a distinct group, sexual differences are present, not on the telson, but on the edges of the uropods.

In *Porcellana longicornis* and *P. platycheles* the fifth abdominal pleuron has a distinguishing sex character. Its margin is crenulated and so differs from that in other Galatheidea.

INTEGUMENT

The integument is divided into two primary layers, both by its mode of formation and by its chemical composition (Yonge (133)). The outermost layer, or cuticle, is without visible structure and is composed of protein with contained lipin derived from the tegumental glands (Yonge (133)). The underlying layer is composed of a number of laminae of chitin which may be secondarily impregnated with calcium salts to form the hard integument. When not so impregnated this layer is flexible as seen in the cardiac fore-gut and in the arthro-dial membranes.

The sub-divisions of these primary layers is based mainly on the work of Vitzou (123), who divided the integument into four zones, the cuticle, the pigmented layer, the calcified layer, and the non-calcified layer. The terminology of these zones has been modified by Drach (37), who tried to bring it in line with that for insects, but this attempt was not altogether satisfactory and it

has been thought advisable to retain the terminology of Vitzou in the present work.

The Cuticle (Epicuticle of Drach) is laid down, according to Yonge (133), by the tegumental glands. It is hyaline and without visible structure although it may have a hexagonal pattern imposed upon it by the underlying pigmentary layer (Figs. 66, 69, pi.). It varies considerably in thickness in the different regions of the body, ranging from 0.2μ in the hind gut to 1.5μ in the pleopods of the female. Yonge has shown the cuticle to be different in its chemical nature from the underlying layers and this gives rise to characteristic staining reactions. Over the carapace little or no cuticle is visible except in the deep sutures and then only the very thinnest layer is present. Setae stain in the manner characteristic of the cuticle.

The Pigmented Layer (Pre-exuvial layer of Drach) is laid down prior to the moult and is the only layer where pigment is found (Figs. 65, 67, 68, pi.). This layer is derived from the underlying epidermal cells and is found only where hardening by calcium impregnation has taken place. It is composed of extremely fine horizontal lamellae which are broken in the upper half of the layer by vertical lines. These lines are spaced at a distance of 6μ to 10μ apart (Figs. 65, 68), and the lamellae joining two vertical lines are seen to curve towards the outside. In sections cut parallel to the surface the vertical lines are seen to form the boundaries of hexagonal areas (Fig. 66), a pattern which suggests that this layer is directly derived from the underlying epidermal cells. In the lower half of the pigmented layer the lamellae from adjoining cells fuse much more readily than in the upper half, so that vertical lines are absent from this portion. Vitzou (123) noticed the vertical lines and observed that in *Homarus* fusion of the chitinous products from adjoining cells took place very readily so that it was impossible to distinguish vertical divisions except at the very beginning of the process of chitin formation. In *Palinurus* the vertical divisions are very evident, Yonge (133). In *Cancer*, according to Pearson (99) and Vitzou (123), vertical divisions are continuous throughout the whole thickness of the calcified integument.

The **Calcified Layer** (Post-exuvial Principal layer of Drach), when fully developed occupies two-thirds of the total thickness of the integument. It is laid down after moulting and is richly impregnated with calcium salts. It again consists of horizontal lamellae, more closely set towards the outside (Fig. 65, c.l.).

The **Non-Calcified Layer** (Post-exuvial Membranous layer of Drach) is very thin and composed of delicate parallel non-calcified lamellae which are not formed until the calcified layer is completed (Figs. 65, n.c.l.).

Where the integument has no calcium impregnation as in the arthrodial membranes, then two layers only are visible. The outer layer is the cuticle and the underlying layer is composed of non-calcified chitin.

The **Epidermis** (Chitinous epithelium of Vitzou) consists of a single layer of columnar cells resting on a basement membrane (Figs. 65, 67, 68, e.). These cells give rise to the chitinous layers of the integument and vary in size both in different parts of the body and during the moulting cycle. During the formation of the new integument the epidermal cells assume gigantic proportions (Fig. 67, e.) and diminish in length as the calcified layer is laid down (Fig. 65, 68, e.).

The **Dermis** lies below the epithelium and consists mainly of scattered cells and connective tissue fibres. The muscle fibres stretch across the dermis and are attached to the inner side of the epidermal basement membrane (Figs. 65, 67, 68, d.m.).

Tegumental Glands (Plate IX, Figs. 70, 71)

The tegumental glands have been described by many authors, Farkas (41, 42) giving a very detailed account. As the tegumental glands found in *Galathea* conform with those found in other Decapoda only their general character need be outlined.

In *Galathea* each tegumental gland consists of a spherical cluster of cells (Figs. 70, 71, t.gl.), each of which has a nucleus situated basally (Fig. 70, n.t.gl.). Each cell discharges its secretion into a centrally situated main duct. This duct (Fig. 70, d.t.gl.) is intracellular in nature and discharges the secretion of the gland through

the integument to the outside. The glands appear to be scattered all over the body and are particularly concentrated in the buccal region and in the female pleopods. Yonge (133) ascribes to the tegumental glands the function of laying down the cuticle, which is spread in a fluid state over the chitinous layers and subsequently hardens. Drach (37) does not agree with Yonge on this point.

In regions where the pigmented layer is present the glands are only found singly, which probably accounts for the thinness of the cuticle in such regions.

In the pleopods of the female and again at their base, a large number of tegumental glands are seen (Fig. 71, t.gl.) with their ducts travelling up the leg towards the non-plumose setae to which the eggs are attached. The tegumental glands in an ovigerous female *Galathea* were not observed in such quantity as those found in *Homarus* by Yonge (135).

In the statocyst (*vide* page 106) the secretion of tegumental glands is probably also employed for the attachment of the statoliths to the statocyst hairs as shown by Lang and Yonge (72).

Ecdysis (Plate IX, Figs. 65, 67, 68, 69)

Drach (37) has clearly shown for *Cancer* that there are four main periods during the moulting cycle and these main periods have been again subdivided. The same periods are found in *Galathea* and so a brief description only will be given.

Period A (Fig. 67) immediately follows exuviation. The integument is soft and formed of only two layers, the cuticle and the pigmented layer. The period ends when absorption of water ceases and the animal is able to stand on its legs.

Period B. The shape of the carapace can now no longer be altered and although it does not give under light pressure, it can be bent without breaking. The whole ventral surface is still soft. The calcified layer has just started to form.

Period C (Figs. 68, 65) is the long inter-moult period during which the tegumentary skeleton is hard. The formation of the calcified layer is completed during the first few weeks and its

completion is followed by the appearance of the non-calcified layer.

Period D (Fig. 69) is preparatory to moult and is completed when the lower part of the calcified layer of the old integument has been absorbed and when the layers characterising Period A have been formed beneath the old integument.

The duration of each period has not been fully ascertained owing to the difficulty of keeping the animals in captivity, and collection on the shore is not practicable except at very low tides. Sexually mature specimens of *Galathea* appear to have a seasonal moult in September-October, when the seasonal sexual characters are lost (*vide* page 27). The next general moult appears to take place in January-February (5 months), when the sexual characters are again acquired. The female lays twice during the season but ecdysis does not appear to take place between the two layings. The pleopods are merely cleaned in preparation for the attachment of a second brood (May-July). The number of moults in the immature specimens, or the duration of the inter-moult period is not known.

Radical changes in the nature of the epidermal cells take place during the moult cycle. Shortly prior to the moult the epidermal cells elongate to about five times their original length (Fig. 67), but shortly after exuviation shrinkage begins with the laying down of the calcified layer (Fig. 68). On the completion of Period C the cells regain their normal size (Fig. 65).

Setae (Plate IX, Fig. 67, Plate XIX, Figs. 115, 116, 117).

There are two main types of setae grouped according to their function and morphology.

- (a) Mechanical setae.
- (b) Sensory setae.

Mechanical Setae have no core of living tissue and are varied in shape according to their function. They occur in the stomach and Yonge (131) has shown that in *Homarus* they are composed of chitin with a very thin outer coating of cuticle.

Sensory Setae (Figs. 67, 115, 117) contain living tissue

which usually extends some distance into the seta from the base ; the seta is supplied with nerve elements. These setae occur over most external parts of the body and in the statocyst (*vide* page 106). In the carapace, glands of considerable size, which look like bunches of grapes, lie at the bases of these setae (Fig. 67, gl.). On the outer flagellum of the antennule are large hair-like setae with very thin walls. These are the olfactory setae (Figs. 116, 117, olf. s.).

PART II

INTERNAL ANATOMY OF *GALATHEA SQUAMIFERA*

THE MUSCULAR SYSTEM

R. J. Daniel (31, 32) made a very complete study of the abdominal musculature of certain Malacostraca, including a detailed study of the abdominal muscles of *Homarus vulgaris* (L.) and *Palinurus vulgaris* (Latr.). Milne-Edwards, in 1834 (83), also gave a fairly detailed general study of the abdominal muscles of *H. vulgaris*, but the description is made more difficult to follow owing to the fact that the publishers did not include Figs. 4, 5, 6, to which frequent references are made by Milne-Edwards.

No work has been found on the musculature of *Galathea* or its near relatives *Munida* and *Porcellana*. It is proposed to give a detailed description of the muscles of the abdomen and gastric mill in *Galathea squamifera*, with a more general description of the muscles serving the limbs, as these are in general similar to those found in other Decapoda.

To keep the work comparable with that of Daniel, the same terminology and scheme has been employed, but the diagrams are less schematic and it is hoped that they will prove a little easier to follow.

[*Method.*—Daniel preserved his material in 70 per cent. alcohol and 4 per cent. formaldehyde, and this is probably better than formaldehyde or alcohol alone. It was found that specimens preserved in formaldehyde were difficult to dissect as the muscle

attachments to the segments were very firm. This hindered clean dissection and in addition, the white flesh was very tiring to the eyes. To overcome this, Daniel stained lightly with eosin, but this was not found to be very helpful.

Owing to the shrinkage and yellowing effects of alcohol on preserved specimens, the muscles tend to part into their respective bundles, and this combined with the yellow tone facilitated dissection. It was necessary, however, to check certain attachments to the integuments in formaldehyde preserved material.]

Abdominal Muscles

The abdominal muscles may be conveniently grouped into the following series :—

- The Ventral Muscles.
- The Superficial Ventral Muscles.
- The Dorsal Muscles.
- The Lateral Muscles.

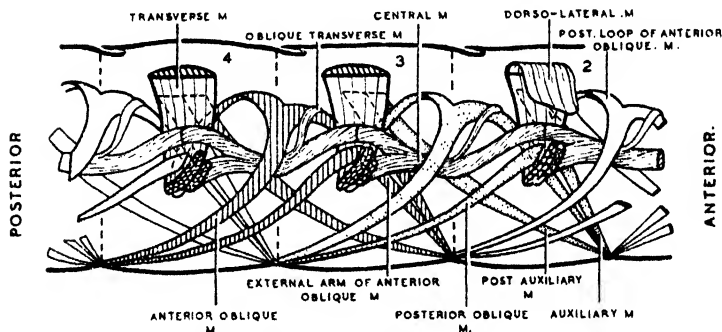
The function of these muscles can be no more than suggested in this work as literature on detailed function is not available. The ventral muscles form the main solid mass of the abdomen and are concerned with its flexure. Underlying these muscles are the weak superficial ventral muscles joining two successive sterna, but owing to their weak nature they can aid but little in the abdominal flexure.

The dorsal muscles lie above the ventral muscles. They are weaker and are concerned with the extension of the abdomen. The lateral muscles are inconspicuous and form merely a weak link between the thorax and the lateral tergal edge of the first abdominal segment.

The Main Ventral Muscular System of a Typical Malacostracan is divided into two parts :—

- i. Thoracico-abdominal Muscles. These arise from the ventral side of the first abdominal segment, and pass anteriorly to their attachments to the endosternites of the thoracic segments.

2. The Ventral Abdominal Muscles. These are a complicated interwoven mass forming the main bulk of the abdominal muscles. It is thought advisable to give a description of the ventral abdominal muscles found in a typical Malacostracan so that the general plan may be understood. The modification found in *Galathea* can then be better appreciated and compared with the modification found in *Homarus*. To this end Text-Fig. 3, and the general description of the muscles concerned, has been reproduced from Daniel's excellent work, as it is felt that this description cannot be bettered; this is as follows :—



TEXT-FIG. 3

Diagrammatic representation of the Ventral Muscles in a typical Malacostracan. View from the medio-lateral aspect showing muscle attachments and courses. (After Daniel (31)).

A Transverse Muscle connects both sides of each abdominal segment. This is present as a stout cross muscle in the more anterior portion of each segment, and has insertions into the two dorso-lateral portions of the tergum. The muscle has a considerable dip to the median line of the abdomen and here there is a vertical cross-tendon that forms a break in the muscle fibre. A similar tendon occurs in all the muscles which run transversely from one lateral half to the other. The Transverse Muscle itself may be strengthened by branches from the central muscles and the posterior loops of the anterior oblique muscles.

The Central Muscle. The name "Muscle Central" was given originally by Milne-Edwards (83) to paired longitudinal muscles in the lobster. These rest with their ends upon adjoining transverse muscles and are therefore actually intersegmental in position. They may, by end to end junctions, form two continuous muscle series, which curve posteriorly into the median line of the abdomen and lie on the anterior face of the transverse muscle.

The **Posterior Oblique Muscle** is joined both to the transverse and central muscles at its anterior end. Occupying two segments, it shares a common insertion with its corresponding anterior oblique muscle.

The **Anterior Oblique Muscle** may be regarded as the most important of the longitudinal muscles. Its main portion lies mesial to the adjacent central muscle, and in the mid-line of the abdomen its broad face is actually pressed against that of the similar oblique muscle of the opposite side of the segment. From this area is given off the posterior loop of the anterior oblique muscle which, after passing lateral to the central muscle, becomes fused to the transverse muscle and joins its fellow in the median sagittal plane of the segment. The anterior oblique muscle traverses two complete segments in a caudad direction before being inserted into the posterior edge of the second one.

The **External Arm of the Anterior Oblique Muscle** rides over the central muscle and runs in a lateral position to the anterior edge of the segment. Its actual origin is immediately in front of this edge and at the common insertion of the paired anterior and posterior oblique muscles which have arisen in more anterior segments.

The **Oblique Transverse Muscles** arise near the junction of the anterior oblique muscle with its external arm, these muscle fibres sweep in between the oblique muscle itself and the central muscle and become joined to the latter. There may be only a few fibres forming a slip, or a robust muscle may be present.

The **Auxiliary Muscles of the Anterior Oblique Muscle** are two muscles which have a common origin with the external arm and in fact are fused to it at the anterior ends.

The auxiliary muscle proper is situated immediately anterior to the arm ; it is lateral in position and, apart from its origin, is confined to its own segment where it becomes attached alongside the transverse muscle.

The Posterior Auxiliary Muscle is also a lateral muscle and runs in a postero-dorsal direction across its segment ; the muscle is adjacent to the transverse and auxiliary muscles of the following segments.

The Dorso-lateral Muscles occur in the Eucarid forms.

The Main Ventral Muscular System of *Galathea* (Plates X, XI, Figs. 72-75).

1. The Thoracico-abdominal Muscles form a unit which arises from the ventral side of the first abdominal segment, and is attached to the thoracic endophragmal bridge. The unit divides into two parts. One part is attached to the dorsal side of the endophragmal bridge, *Thoracico-abdominal Muscle 1* (Fig. 73, 1a), and the other to the ventral side, *Thoracico-abdominal Muscle 2* (Fig. 73, 1b).

This is a much simpler arrangement than that found in *Homarus*, where five muscles arising from the first abdominal segment are attached to endosternites 1-6.

2. The Ventral Abdominal Muscles (Figs. 72-75), as already mentioned form the main mass of the abdominal muscles. Most conspicuous are the anterior oblique muscles with which the description will begin. In order to observe the underlying muscles, the Anterior Oblique Muscles must first be removed.

ANTERIOR OBLIQUE MUSCLES

According to Daniel (31), the most anteriorly placed anterior and posterior oblique muscles in *Homarus* compare in disposition with the second pair found in *Crangon* and *Praunus*. The first pair in *Homarus* therefore is referred to as anterior and posterior oblique muscle 2. This is also true of *Galathea*, and so the first pair will also have the same numbering.

There are anterior and posterior oblique muscles for segments 2-6, and anterior oblique muscles only for segments 6-7.

Anterior Oblique Muscle 2 (Plates X, XI, Figs. 72-75, IIa) takes its origin from a lateral attachment to the first transverse muscle (Figs. 72, 73, VIIa). It passes under the first central muscle (Figs. 72, 73, VIa) into the median line, and continues posteriorly to its attachment on the ventral side of the second segment.

Anterior Oblique Muscle 3 (Figs. 72-75, IIb) is attached to the external arm (Fig. 74, IVb) which originates laterally in segment 1, and is attached ventrally to the thoracico-abdominal muscle 1b. From its attachment to the external arm, anterior oblique muscle 3 passes posteriorly over central muscle 2 (Figs. 72, 73, VIb) to become attached ventrally to segment 3.

Anterior Oblique Muscle 4 (Figs. 73-75, IIc) is essentially similar to anterior oblique muscle 3. It originates also in the external arm of segment 1 (Fig. 74, IVc), which is the attachment of the thoracico-abdominal muscle 1a. Finally it becomes inserted on the ventral side of segment 4.

Anterior Oblique Muscle 5 (Figs. 72-75, IId) is similar to muscle 4. The external arm (Fig. 74, IVd) originates in segment 2, which is the joint insertion of anterior and posterior oblique muscle 2 (Fig. 73, IIa). It then passes backwards to its attachment on the ventral side to segment 5.

Anterior Oblique Muscle 6 (Figs. 72-75, IIe) differs from the preceding one in that fibres are given off to the external arms of both segments 2 and 3 (Fig. 74, IVd, IVe).

Anterior Oblique Muscle 7 (Figs. 72-75, IIIf) originates in the external arm of segment 4 (Fig. 74, IVf), and passes mesial to the last central muscle (Fig. 73, VIIf) to its attachment in segment 6.

AUXILIARY MUSCLES TO THE ANTERIOR OBLIQUE MUSCLES (Figs. 72, ve, vf; Fig. 74, vc-vg)

Each of the external arms of the anterior oblique muscles 3-7 is accompanied by an auxiliary muscle sharing the same origin. This muscle is lateral in position and passes in a postero-dorsal direction where it becomes attached to the integument of that segment.

Auxiliary Muscle 1 (Fig. 74, vb) is attached to the external arm of the anterior oblique muscle 3 (Fig. 74, iib) and caps the posterior extension of the first central muscle (Fig. 73, v1a). It is attached by its anterior edge to the first transverse muscle (Fig. 73, viia), and by its posterior edge to the second central muscle (Fig. 73, vib). The second central muscle is therefore inserted between the first auxiliary muscle and the external arm of anterior oblique muscle 3. The same relationship occurs with central 6 (Fig. 73, v1f) and auxiliary muscle 5 (Fig. 74, vf).

Auxiliary Muscles 2, 3, 4 (Fig. 74, vc-ve) lie lateral to their corresponding external arms. The central muscle in each case is inserted anteriorly to the auxiliary muscle, and not between the auxiliary muscle and the external arm as in vb and vf.

Auxiliary Muscle 6 (Fig. 74, vg) overlaps the posterior dorsal half of the central muscle 6 (Fig. 73, v1f) and is another muscle resembling an external arm (Fig. 74, vg). As there is no anterior oblique muscle making contact with this muscle it is considered to be a modified member of the above series as in *Homarus*.

POSTERIOR OBLIQUE MUSCLES (Figs. 72-73, iiaa-iiid).

There is one posterior oblique muscle in each of the four anterior abdominal segments. They arise with their anterior oblique muscles from the ventral side and terminate anteriorly in the next segment but one.

Posterior Oblique Muscle 2 (Figs. 72, 73, iiaa) is connected ventrally to anterior oblique muscle iia (Fig. 73). Anteriorly it splits into two strips, one of which lies against central muscle v1a, and the other embeds itself into the connection between the posterior extension of central muscle v1a, and the central muscle vib (Fig. 73).

Posterior Oblique Muscles 3, 4, 5 (Fig. 73, iib-iiid) are attached ventrally to anterior oblique muscles 3, 4, 5 (Fig. 73, iib, iic, iid), whilst their anterior terminations rest against the central muscle of the previous segment.

CENTRAL MUSCLES (Figs. 72, 73, via-vif).

The central muscles, like the transverse muscles, are confined to a single segment except for segment 1. They act as supporting saddles to the various anterior oblique muscles. In *Homarus* these muscles are joined end to end to form a continuous rope as in Text-Fig. 3, and give subsidiary support to the transverse muscles. In *Galathea* the main bulk of transverse muscles viia-viie is composed of fibres from the central muscle.

Central Muscle 1 (Figs. 72, 73, via) is attached anteriorly to the dorsal side of the thoracic endophragmal bridge. It passes lateral to the thoracico-abdominal muscle 1a, and then curves into the median line where it shares equally in the formation of the first transverse muscle (Fig. 73, viia). From the posterior dorsal surface a fairly strong connection passes mesial to the first auxiliary muscle, and makes contact with central muscle 2 (Fig. 73, vib).

Central Muscle 2 (Figs. 72, 73, vib) is confined entirely to the first segment. It has its origin in the lateral walls between the external arm of the anterior oblique muscle 3 and its auxiliary muscle. It forms the major portion of the second transverse muscle (Fig. 73, viib) and has a dorsal connection with the external arm of the anterior oblique muscle 3. The anterior end of the posterior oblique muscle 2 forms a deep groove in the central muscle into which it penetrates.

Central Muscles 3, 4, 5 (Figs. 72, 73, vic-vie) are all similar to central muscle 2 except that they are not penetrated by the posterior oblique muscles.

Central Muscle 6 (Fig. 73, vif) is longer than the preceding four muscles with a lateral penetration between the external arm of the anterior oblique muscle 7 and its auxiliary muscle. It is overlapped on the postero-dorsal half by the modified auxiliary muscle (Fig. 74, vg, Fig. 75, vi).

TRANSVERSE MUSCLES (Figs. 72, 73, viia-viie).

As already stated in the general description the transverse muscle is joined by fibres from the central muscle and posterior loop of the anterior oblique muscle. In *Galathea* there are no

posterior loops and except in the first segment the main bulk of the transverse muscle is made up of fibres from the central muscle. In this it differs markedly from that of *Homarus* where the central muscle support is subsidiary to the transverse muscle, and where dorso-lateral muscles are present, arising from broad horizontal insertions in the lateral wall. In *Galathea* these insertions are small and dorso-lateral muscles are absent.

Transverse Muscle 1 (Figs. 72, 73, VIIa) is united laterally with the looped portion of anterior oblique muscle 2, while the dorsal half is formed from the transverse portion of central muscle 1 (Fig. 73, VIIa).

Transverse Muscle 2 (Figs. 72, 73, VIIb) has a small vertical dorso-lateral insertion to the integument between central muscle 2, and the external arm of the anterior oblique muscle 3. The major dorsal portion is composed of the transverse fibres of the central 2 (Fig. 73, VIIb).

Transverse Muscles 3, 4, 5 (Figs. 72, 73, VIIc-VIIe) are similar to transverse muscle 2.

There is no true transverse connection in the sixth abdominal segment.

Summary of Main Ventral Muscular System

From the phylogenetic scheme proposed by Daniel (32) it may be observed that in the main ventral system there are points of general agreement, and these may be taken as expressing a relationship. Further, Daniel says that it has been assumed that similar changes in different systems have happened at a particular time, and to the same degree. Thus the posterior auxiliary muscles are held to disappear suddenly and at the time of appearance of the dorso-lateral muscles. It was thought therefore that it might be possible to ascertain at what period *Galathea* branched away from the *Homarus* stock.

A review of the muscles in the main ventral system of *Galathea* and *Homarus* shows that when the same muscles are present in both species they agree closely in number if not in size. This therefore suggests relationship with *Homarus*, but three sets of muscles found in *Homarus* are absent in *Galathea* :—

1. Posterior Loop of Anterior Oblique Muscle.
2. Oblique Transverse Muscle.
3. Dorso-lateral Muscles.

If one considers the phylogenetic scheme proposed by Daniel (32) it will be noted that along the *Homarus* line the appearance of

SUMMARY OF THE MUSCLES PRESENT IN THE MAIN VENTRAL
SYSTEM OF *GALATHEA* AND *HOMARUS*.

| Muscles. | <i>Galathea</i> . | <i>Homarus</i> . |
|--|--|---|
| ANTERIOR OBLIQUE MUSCLE showing the occurrence and manner in which they are linked together in series. | - - - 4 - - 7 - - 2 - - 5 - - - - - 3 - - 6 - - | - - - 4 - - 7 - - 2 - - 5 - - - - - 3 - - 6 - - |
| ANTERIOR OBLIQUE MUSCLES consisting of a median portion joined directly to an EXTERNAL ARM. | - - 3 4 5 6 7 - | - - 3 4 5 6 7 - |
| POSTERIOR LOOP OF ANTERIOR OBLIQUE MUSCLES. | Absent | - 2 3 4 5 6 7 - |
| POSTERIOR OBLIQUE MUSCLES. | - 2 3 4 5 - - - | - 2 3 4 5 - - - |
| AUXILIARY MUSCLES. | - 2 3 4 5 6 - - | - 2 3 4 5 6 - - |
| OBLIQUE TRANSVERSE MUSCLES. | Absent. | - - 3 4 5 6 - - |
| CENTRAL MUSCLES. | 1 Linked to 2 by posterior process. 3 4 5 6 segmental not linked. | 1 2 3 4 5 Linked in longitudinal series. 6 not linked. |
| TRANSVERSE MUSCLES. | 1 2 3 4 5 - - - 1 Thoracic Transverse Muscle attached to Anterior Oblique Muscle 2. | 1 2 3 4 - - - - |
| DORSO-LATERAL MUSCLES. | Absent. | - 2 3 4 - - - - |
| POSTERIOR AUXILIARY MUSCLE. | Absent. | Absent. |

dorso-lateral muscles and the absence of thoracic central muscles is established. In *Galathea* there are no dorso-lateral muscles and the first central muscle continues forward to its attachment to the endophragmal bridge. This can hardly be termed a thoracic central muscle as it is due to modification in the endophragmal system. It appears doubtful therefore if *Galathea* branched away from the main stock at this juncture owing to specialised modification that has taken place during evolution. Daniel (32) also states that the musculature of *Meganyctiphanes norvegica* is highly modified in that the longitudinal muscles are broken up segmentally, and each of them contributes to a powerful transverse muscle. A similar condition is also found in *Galathea*.

Galathea appears therefore to have characters common to several types, and no definite point of departure from the stem giving rise to *Homarus* can be indicated.

Superficial Ventral Muscles (Plate XI, Fig. 77)

There are two pairs of superficial ventral muscles in the thorax and first abdominal segment. One muscle from each pair remains lateral, whilst the other passes inwards to a median connection with the sternum. In the second abdominal segment the lateral member is missing.

The Lateral Thoracic Superficial Ventral Muscle (Fig. 77, th.s.v.m. 1) remains in a lateral position and becomes attached posteriorly to the lateral ventral edge of the first sternum. The inner muscle (Fig. 77, th.s.v.m. 2) becomes attached in the median line to the sternal bar of the first abdominal segment. Continuing backwards from this point are two muscles which diverge to their somewhat lateral connection with the second abdominal sternal bar. These are the Median Abdominal Superficial Ventral Muscles (Fig. 77, ab.s.v.m. 1).

Joining the lateral margins of the first abdominal sternal bar are the Lateral Abdominal Superficial Ventral Muscles (Fig. 77, ab.s.v.m. 2).

This series is repeated in the third abdominal segment for the median abdominal superficial ventral muscle only.

From the cross formed by the median thoracic and median abdominal superficial ventral muscles a pair of Transverse Superficial Ventral Muscles (Fig. 77, ab.t.s.v.m.) pass outwards to their attachment to the lateral walls of the fifth thoracic sternum.

This system only resembles *Homarus* in having a median and lateral pair of muscles to each segment. Evolutionary modification in the abdomen has caused discontinuation of the segmental arrangement found in other Malacostraca.

DORSAL MUSCLES (Plate XI, Fig. 76)

The dorsal muscles may be grouped into superficial dorsal muscles and deeper main dorsal muscles.

The Main Dorsal Muscles (Fig. 76, m.d.m. 1, 2, 3) are arranged in three series. The median and broadest of these series (Fig. 76, m.d.m. 1) consists of a twisted pair of muscles joined end to end segmentally to form a continuous broad band. The band is attached anteriorly to the thoracic endopleural supports (Plate III, Fig. 14, e.pl. 8p., ext.ep. 9) and passes back to its posterior attachment to the anterior edge of the sixth abdominal segment. In each segment fibres are given off to dorsal tergal attachments.

The second series (Fig. 76, m.d.m. 2) is ventrolateral to the median series in its anterior attachment to the posterior edge of the extension of the ninth epimeron (Plate III, Fig. 14, ext.ep. 9). The abdominal portion lies lateral to the median series, and is neither so twisted nor so thick. It is attached posteriorly to the sixth abdominal tergum alongside the median series.

The third series (Fig. 76, m.d.m. 3) lies ventrolateral to the second series, and is similar to it, but not so twisted.

The Median Dorsal Superficial Muscle (Fig. 75, m.d.s.m.) consists of a few fibres attached to the anterior edges of two successive abdominal terga. They can have little function and are most clearly seen in the fourth and fifth segments.

LATERAL SUPERFICIAL MUSCLES (Plate XI, Fig. 76, l.th.m.)

No obvious lateral superficial muscles are visible, but arising from the lateral tergal edge of the first abdominal segment are two

muscles which pass dorsally into the thorax. These probably represent the Outer Lateral Thoracic Muscles (Fig. 76, l.th.m.).

In Daniel's work the evolutionary evidence yielded by comparison of the dorsal superficial muscles of the Malacostraca is somewhat uncertain and cannot be at present reconciled with the evidence obtained from the main ventral system.

There are three series of muscles present in the dorsal system of both *Galathea* and *Homarus*, but beyond this, comparison is not helpful and no additional evidence can be obtained from the dorsal thoracic muscles.

Muscles controlling the telson and uropods are shown in Fig. 78.

Muscles of the Cephalothorax (Plate XI, Figs. 75, 76, Text-Fig. 4)

The muscles of the Cephalothorax differ but slightly from those found in any other decapod. They have been dealt with very adequately by Pearson (99) and others, and it is proposed, therefore, to do no more than indicate these muscles in Figs. 75, 76. The account of the muscles of the fore-gut will be found in the section on the alimentary canal, following the description of the ossicles to which they are attached.

Owing to the peculiarities of the endophragmal system of *Galathea* it is considered advisable to deal a little more fully with the muscles of the pereopods.

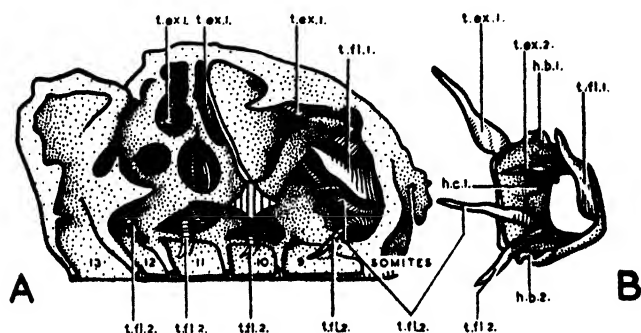
MUSCLES OF THE FIRST PEREIOPOD OR CHELA (Text-Fig. 4 ; Plate X, Fig. 74 ; Plate VI, Fig. 36).

Coxa. There are two muscles—a more lateral posterior extensor pulling the limb away from the body, and an anterior flexor pulling the limb towards the body.

The **Extensor** is situated in the ninth pleural muscle chamber beneath epimeron 9 (Plate III, Fig. 15, ep. 9). The muscle arises from both walls of the chamber, and passes forwards and downwards to its insertion in the long extensor tendon (Text-Fig. 4, A.B, t.ex.I, somite 9).

The **Flexor** is a much larger muscle and is situated in the ninth sternal chamber. It arises from strong connections with the endophragmal bridge and with the ninth endopleural support (Plate III, Fig. 14, e.pl. 9a). It then passes forwards and downwards to its insertion on the broad tendon on the anterior face of the coxa (Text-Fig. 4, B, t.fl. 1).

The **Basis** has anterior and posterior flexor and extensor muscles. Both flexor muscles are powerful and attached to strong tendons, while the posterior extensor muscle is reduced.



TEXT-FIG. 4

Thoracic endophragmal system seen from the median line and showing the tendons of attachment for the muscles of the pereopods. $\times 6$

t.fl.1, tendon for attachment of coxal flexor muscle; *t.ex.1*, tendons for attachment of coxal extensor muscle; *h.b.1*, dorsal hinge of coxa; *h.b.2*, ventral hinge of coxa; *h.c.1*, posterior hinge of basis; *t.fl.2*, tendons for flexor muscles of basis somites, 9, 10, 11, 12; *t.ex.1*, tendon for extensor muscle of coxa; *t.ex.2*, tendon for extensor muscle of basis.

The **Anterior Extensor** is situated lateral to the flexor muscle of the coxa and attached to the ninth endopleural support (Plate III, Fig. 15, ep. 9). It runs forwards to its insertion in the tendon immediately above the anterior hinge of the basis (Text-Fig. 4, B, t.ex. 2).

The **Posterior Extensor** is contained within the basis and attached to a small tendon above that of the anterior extensor.

The **Anterior Flexor** (Plate X, Fig. 74, m.fl. 2) lies in the ventral region of the ninth sternum and is attached to the ventral side of the endophragmal bridge (Fig. 74, m.fl. 2, somite 9).

It passes forwards and upwards to its tendon attachment (Text-Fig. 4, A B, t.fl. 2, somite 9).

The **Posterior Flexor** (Text-Fig. 4, A B, t.fl. 2, somite 9) lies in the same epimeral chamber as the extensor for the coxa (t.ex. 1), but is situated mesial to it.

In pereipods 2, 3, 4, the same arrangement holds for both coxa and basis, and Text-Fig. 4 shows some of the tendons of attachment in relation to the endophragmal system. Little can be seen in Fig. 74 of the muscles except those situated above sterna 10, 11, 12, which are attached to their corresponding tendons (Text-Fig. 4, t.fl. 2, somites 10, 11, 12). The four sheets of muscle, seen in Fig. 74 above the anterior flexor muscles just mentioned and covering the endophragmal system, are also attached to the flexor tendons of the basis.

Histology of Muscle

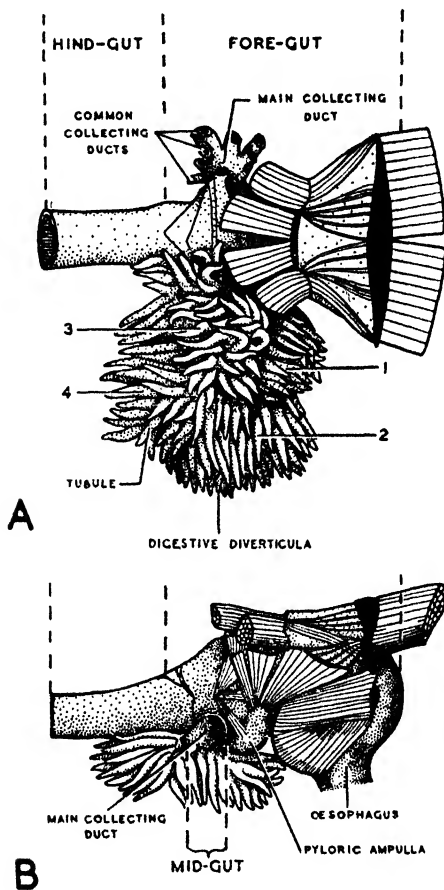
The histology of the striped muscle of *Galathea* is identical with that found in other decapods. The details of Crustacean muscle have been given previously by numerous authors. With chlorazol black E (1 per cent. in 90 per cent. alcohol), or with Weigert's iron haematoxylin and van Gieson's (picro-säurefuchsin), the structure may be clearly seen.

Pearson (99) states that in fresh muscle of *Cancer* some of the muscles are yellower than others. The darker muscles are those with the most persistent or strenuous action, and have more sarcoplasm than the lighter muscle. This has not been noted to any extent in *Galathea*.

THE ALIMENTARY CANAL

The alimentary canal is divided into three regions, fore-, mid- and hind-gut, and extends from the mouth to the anus. The mouth is placed dorsal to the mandibles on the ventral side and leads directly into the oesophagus, which soon dilates to form the stomach, gastric mill or gizzard. The oesophagus and stomach constitute the fore-gut and its lining is continuous with the integument, a condition which is also found in the hind-gut, while the mid-gut, which lies between these two regions, lacks this lining. In *Galathea*

squamifera the mid-gut is so reduced that it is virtually composed of the opening of the digestive diverticula (Hepato-pancreas), since only the area immediately around the opening of the diverticula lacks a chitinous lining (Text-Fig. 5).



TEXT-FIG. 5

A., dorsal view of the anterior end of the alimentary tract of *Galathea squamifera*, showing the division into fore and hind-gut, the four lobes of the mid-gut digestive diverticula (1-4), the collecting ducts and the tubules.

B., lateral view of A, with the digestive diverticula removed to reveal the entrance of the main collecting tubule into the mid-gut. $\times 2$

In the decapods, Yonge (131, 132, 134) shows that not only does the secretion of the digestive enzymes take place extensively

from cells in the tubules of the digestive diverticula, but absorption of the soluble products of digestion also takes place principally in this region. In *Galathea* the extreme reduction of the mid-gut must make this even more pronounced. Since secretion is forced out of the diverticula and the soluble products of digestion are drawn back into it, some mechanism is necessary for rhythmical contraction and expansion of the tubes. Pump (108) has given a detailed account of the network of longitudinal and circular muscle fibres which surround the tubules. Contraction of the circular muscles forces the fluid from the diverticula forward by definite channels into the gastric mill, while relaxation of these and contraction of the longitudinal fibres causes the digested material to be drawn back through the gland filter (*vide* page 60) into the diverticula.

In addition to the digestive diverticula, the anterior end of the mid-gut of many decapods may give rise to a short unpaired caecum as in the Astacura, or two convoluted tubules as in most Brachyura. Athanassopoulos (5), however, states that he is unable to find these in *Carcinus maenas*, although Pearson (99) describes them for *Cancer pagurus*. In *Callinassa* among the Thalassinidea and in most Paguridea a pair of longer or shorter caeca are present. In most Thalassinidea, however, only a single caecum is given off. In the Galatheidea and in *Paguristes* (Paguridea) no caecum is found in the adult, but Williams (128) has observed a short blind diverticulum in the pre-zoea of *Porcellana platycheles*. *Dromia* possesses a short caecum and so in this respect resembles more closely the Astacura or Thalassinidea than the Brachyura.

From the posterior end of the mid-gut, or extreme anterior end of the hind-gut, another unpaired caecum of considerable length is found in the Brachyura. A short caecum is found in the Astacura, the Thalassinidea and in some Paguridea, but is absent in the Galatheidea.

The Fore-Gut (Plate XII, Figs. 79-82 ; Plate XIII, Fig. 83).

The fore-gut is subdivided into an oesophagus and a stomach or gizzard. The lining of the oesophagus is continuous with the

integument and is formed of two layers, an outer staining red, presumably cuticle, and an inner chitinous layer staining blue with Mallory's connective tissue stain. Beneath this integument are tall columnar cells resting on a basement membrane. Below this, connective tissue and tegumental glands are found, the whole being surrounded by a layer of circular muscle (Fig. 83, c.o.e.). Attached to the basement membrane and passing through the connective tissue and circular muscle layer are the dilator muscles of the oesophagus (Fig. 83, l.o.e.d.).

The stomach is also divided into a spacious grinding anterior portion and a narrower filtering posterior portion. The terms cardiac and pyloric fore-gut applied respectively to these portions by earlier authors are misnomers, but merit retention by virtue of their extensive use (Yonge (131)) and also because the nomenclature of the ossicles in these regions still refers to this old terminology.

When the food has been sufficiently ground by the teeth of the cardiac fore-gut and acted on by enzymes from the digestive diverticula it is passed on by way of the cardio-pyloric valve (*vide* page 54) to the pyloric fore-gut. As the function of the pyloric fore-gut is that of a filter it is only thickened by supporting ossicles and is divided into dorsal and ventral compartments by means of two lateral folds. These folds project into the lumen forming two supra-ampullary ridges ("voute ampullaire" Mocquard (85)). Coarse material passes into the dorsal chamber, while the fine material passes into the ventral chamber through two sieve-like processes called the gland filters.

The Ossicles of the Fore-Gut (Plate XII, Figs. 79-82)

A special nomenclature for the ossicles of the fore-gut was first introduced by H. Milne-Edwards (83). Huxley (65) and Mocquard (85) adopted this nomenclature in the main and extended it. Nauck (89) and Albert (1) have not followed this lead.

Although the terms employed by Mocquard are not altogether satisfactory, his terminology will be used in the present work.

The ossicles of the cardiac chamber can be divided into two sets :—

- (a) Those taking part in the formation of the Gastric Mill.
- (b) Supporting Ossicles.

(a) OSSICLES OF THE CARDIAC FORE-GUT (Figs. 79-82)

There are ten main ossicles in the cardiac fore-gut situated in the dorsal and lateral walls of the cardiac chamber and in the anterior portion of the pyloric chamber.

For descriptive purposes these can be divided into three groups :—

1. Anterior arch. (3 ossicles).
2. Posterior arch. (3 ossicles).
3. Ossicles connecting the two arches,
 - (a) Lateral connections. (2 ossicles).
 - (b) Median connections. (2 ossicles).

1. Anterior Arch

The largest portion of the anterior arch is formed by the central **Mesocardiac Ossicle** (Figs. 79, 80, 82, m.c.). It is semi-circular, with the posterior portion thickly calcified, while the anterior portion is thin and in places quite membranous. This central ossicle is bounded on each side by a short rod-like **Pterocardiac Ossicle** (Figs. 79, 82, pt.c.).

2. Posterior Arch

Like the anterior arch the posterior arch is composed of a central and two lateral ossicles. The central **Pyloric Ossicle** (Figs. 79, 80, 82, py.) forms a roof to the pyloric chamber and is somewhat drawn backwards to connect with the most anterior of the pyloric supporting ossicles (*vide* page 54). On each side of the pyloric ossicle are two small flat **Exopyloric Ossicles** (Figs. 79, 80, ex.py.).

3. Ossicles Connecting the Two Arches

The anterior and posterior arches are connected laterally by the powerful **Zygocardiac Ossicles** (Figs. 79, 80, 81, 82, z.c.). These articulate anteriorly with the ventral extremities of their corresponding pterocardiac ossicles (pt.c.), while posteriorly each articulates with the exopyloric ossicle (ex.py.) on its own side. The median edges project into the cavity of the cardiac chamber to form the **Lateral Teeth** (Fig. 82, l.t.). Each lateral tooth

consists of a single rounded surface followed by a row of horny ridges embossed on a curved spatula-like extension.

The median connection with the anterior and posterior arch is maintained anteriorly by the transverse part of the "T"-shaped Urocardiac Ossicle (Figs. 79, 80, u.c.), firmly fixed to the posterior edge of the mesocardiac ossicle (m.c.). The horizontal stem passes posteriorly between the two zygo-cardiac ossicles (z.c.) and is attached to the anterior edge of the Median Tooth (Fig. 82, m.t.). To the posterior edge of the median tooth is attached the Prepyloric Ossicle (Figs. 80, 82, pr.p.). This passes obliquely forward and upwards to become attached to the anterior face of the pyloric ossicle (py.), thus completing the median connection.

(b) CARDIAC SUPPORTING OSSICLES

A pair of rod-shaped Pre-pectineal Ossicles (Figs. 79, 82, p.pec.) arise from the posterior edge of each pterocardiac ossicle (pt.c.) and pass backwards below each zygo-cardiac ossicle (z.c.). Each internal posterior end is broadened into a flat head which constitutes the Lateral Accessory Tooth (Fig. 82, l.a.t.). The posterior edge of this head is denticulate and stiffly setose. Each pre-pectineal ossicle (p.pec.) is continued backwards as the Pectineal Ossicle, from the end of which the post-pectineal ossicle (pt.pec.) and the infero-lateral cardiac ossicle (il.) arise.

The Post-pectineal Ossicle (Figs. 79, 82, pt.pec.) is a thin rod with its posterior inner border furnished with stiff setae, while its ventral extremity ends in a setose Lateral Oesophageal Valve (Fig. 82, l.o.v.). The Infero-lateral Cardiac Ossicle (Figs. 79, 82, il.) lies directly beneath the post-pectineal ossicle and is not terminated by a valve. Its inner edge is bordered by a dense comb of fine setae covering the ventral groove.

The Ventral Groove (Fig. 82, v.g.) forms a channel behind this comb of setae and Yonge (1931) states that the secretions of the digestive diverticula are able to pass forwards by way of the cardio-pyloric valve (see below) into this channel.

Arising from the dorsal extremity of the infero-lateral cardiac ossicle (il.) is a small curved *Subdentry Ossicle* (Fig. 79, s.dt.) which passes upwards and curves over the lateral edge of the zygocardiac ossicle (z.c.).

On the lateral walls of the cardiac chamber are two thin *Postero-lateral Cardiac Plates* (Fig. 79, p.cd.pl.) which may be supported on their dorsal and ventral edges by two slim rods.

On the anterior portion of the cardiac fore-gut there is a circular *Cardiac Plate* (Figs. 79, 80, cd.pl.), consisting of slightly thickened chitin divided by a median groove into two halves.

The *Cardio-pyloric Valve* (Fig. 82, c.p.v.) consists of two thickened ridges meeting obliquely in the median ventral portion between the cardiac and pyloric chambers. They are covered by fine rows of low ridges giving a corrugated appearance to the valve. It is also pigmented and this indicates that, in addition to its function of closing the cardio-pyloric opening, it may act as a fourth median ventral tooth.

OSSICLES OF THE PYLORIC FORE-GUT (Plate XII, Figs. 79-82)

The pyloric fore-gut passes backwards from the pyloric ossicle (py.) to the dorsal valve (d.v.). Projecting from the ventral pyloric chamber are two rounded *Pyloric Ampullae* (Figs. 79, 81, p.a.), while along the dorsal side are three ossicles capping a strong chitinous ridge. That nearest the pyloric ossicle is the *Anterior Mesopyloric Ossicle* (Figs. 79, 80, a.m.). This is followed by a triangular chitinous *Posterior Mesopyloric Ossicle* (Figs. 79, 80, p.m.), in which the borders only are strongly calcified. From the posterior corners of this ossicle two strong *Uropyloric Ossicles* (Figs. 79, 80, u.p.) pass in a ventral direction to terminate just above the *Dorsal Valve* (Figs. 79, 80, 82, d.v.).

From the posterior corner of each uropyloric ossicle (u.p.) a *Posterior Pleuropyloric Ossicle* (Figs. 79-81, p.pl.) traverses the postero-lateral sides of the pyloric fore-gut, while a stout *Anterior Pleuropyloric Ossicle* (Figs. 79-81 a.pl.) traverses their antero-lateral walls. It begins beneath the

posterior mesopyloric ossicle (p.m.) and passes obliquely forward to the middle of the sub-dentary ossicle (s.dt.). These two pleuro-pyloric ossicles are joined horizontally by the Middle Pleuro-pyloric Ossicle (Fig. 79, m.pl.), which gives rise on the inside to the pleuropyloric valve (Text-Fig. 6, page 59).

The ventral aspect (Fig. 81) shows the Cardio-pyloric Valve (Fig. 81, c.p.v.) on each side of which are two triangular Antero-inferior Pyloric Ossicles (Fig. 81, a.i.p.). Various small ossicles surround the pyloric ampullae, but these cannot be differentiated as Pearson (99) has done for *Cancer*.

The pyloric fore-gut terminates in four valves, the largest of which is the Dorsal Valve (Figs. 79-82, d.v.). Each side of this is a small setose Lateral Valve (Fig. 82, l.v.), while the under surface ends in a Ventral Terminal Valve (Fig. 82, v.t.v.).

Comparison of the Gastric Ossicles

Mocquard (85), in concluding his work, remarked that for each natural group there is a given type of gastric mill and if the gastric mill of a crustacean placed within that natural group does not conform to type, then that species should be removed from that group.

The following comparison has been drawn up from the works of Mocquard (85), Patwardan (98, parts I-IV), Yonge (131), and Pearson (99).

The gastric mill in Brachyura is characterised by the presence of a small mesocardiac and elongated pterocardiac ossicles.

In the Brachyura, Astacura and Palinura the cardio-pyloric valve is simple and covered with setae and the lateral teeth consist of a number of denticles.

In the Astacura, Palinura and Anomura the mesocardiac ossicle is large and the pterocardiac ossicle small.

The Anomura differ from the Astacura, Palinura and Brachyura in the nature of their cardio-pyloric valve. This is more complicated with low ridges, or denticulate as in *Hippa*. Its horny nature suggests that it may serve as an accessory median ventral tooth. The lateral accessory teeth take the form

of a triangular plate with denticles along the posterior face.

Besides these two very distinctive features, Mocquard (85) also points out that in the Lithodidae, Porcellanidae and Galatheidæ the cardiac discs, the ventral cardio-pyloric valve, the median pleuropyloric ossicle and pleuropyloric valve (*vide* page 60) have common characters which are different from those found in any other group.

The gastric mill of *Dromia* appears to have mixed characters and its affinities with the Anomura do not seem to be close, and Mocquard (85) thinks that it should be joined to the Homolidae.

Muscles of the Fore-Gut (Plate XIII, Figs. 83, 84)

Mocquard's (85) arrangement for dividing the muscles of the fore-gut into the two following kinds has been adopted :—

1. Extrinsic Muscles.
2. Intrinsic Muscles.

Extrinsic muscles are those which have their origin in the exoskeleton and their insertions on the ossicles of the fore-gut.

Intrinsic muscles have both their origin and insertion on the ossicles of the fore-gut.

I. EXTRINSIC MUSCLES OF THE GASTRIC MILL (Figs. 83, 84)

Two strong Anterior Gastric Muscles (Figs. 83, 84, a.g.m.) arise from the procephalic processes beneath the rostrum and pass backwards over the cardiac plates (cd. pl.) to their insertion along the anterior border of the mesocardiac ossicle (m.c.).

Arising from the inner ridge of the cervical groove of the carapace are the Posterior Gastric Muscles. These are divided into two pairs, Internal Posterior Gastric Muscles (Figs. 83, 84, i.p.g.) and External Posterior Gastric Muscles (Figs. 83, 84, e.p.g.). The inner pair terminate on the pyloric ossicle (py.), while the outer pair are inserted on the exopyloric ossicle (ex.py.).

For dilating the cardiac portion of the stomach there are two pairs of Upper Anterior Dilator Muscles (Figs. 83, 84, u.a.d.). The dorsal one originates from the inner side of the orbital plate, while the lower one rises from the lateral

edge of the procephalic process. They are both inserted on to the upper lateral surface of the cardiac discs of the cardiac fore-gut.

In the median line a very weak Lower Anterior Dilator Muscle (Fig. 83, l.a.d.) arises from the anterior margin of the epistome and is attached to the cardiac stomach above the oesophagus. From the posterior lateral border of the branchial chambers two stout Postero-lateral Dilator Muscles (Plate XI, Fig. 76; Plate XIII, Fig. 83, p.l.d.) arise and pass inwards in front of the mandibular apophysis. They then split and are inserted on the anterior and posterior ventral edges of the postero-lateral cardiac plates (cd.pl.).

On the dorsal side of the pyloric chamber two Dorsal Pyloric Dilator Muscles (Fig. 83, d.py.d.) arise from the same origin as the posterior gastric muscles and are inserted on the anterior and posterior mesopyloric ossicles (a.m., p.m.). On each side of the posterior gastric muscles another muscle bundle from the cervical groove passes ventrally and terminates on an ossicle situated on the lateral walls of the dorsal channel of the pyloric stomach. This muscle is not figured in Mocquard and has been termed here for descriptive purposes as the Latero-dorsal Pyloric Dilator Muscle (Fig. 83, l.d.py.d.).

From the under-side of the pyloric stomach anterior to the ampullae an outer and inner pair of Ventral Pyloric Dilator Muscles arise. The Inner Ventral Pyloric Dilator Muscle (Fig. 83, i.py.d.) is the longer. It arises near the base of the mandibular apophysis and passes back to its insertion on the antero-inferior pyloric ossicle (a.i.p.). The Outer Ventral Pyloric Dilator Muscle (Fig. 83, o.py.d.) is shorter. It arises from the fifth epimeron and is inserted lateral to the inner ventral dilator muscle.

The oesophagus is dilated by a Lateral Oesophageal Dilator Muscle (Fig. 83, l.o.e.d.) which arises from the posterior angle of the epistome. Two very weak Posterior Oesophageal Dilator Muscles (Fig. 83, p.o.e.d.) arise from the lateral side of the abductor muscle of the mandibles and are inserted on the postero-lateral border of the oesophagus.

2. INTRINSIC MUSCLES OF THE GASTRIC MILL (Plate XIII, Figs. 83, 84).

On the dorsal surface of the gastric mill are the **Cardiopyloric Muscles** (Figs. 83, 84, c.py.). They consist of three muscles attached anteriorly to the posterior and lateral edges of the mesocardiac ossicle (m.c.). Posteriorly the two inner muscles are attached to the exopyloric ossicles (ex.py.). The median muscles however consist only of a few fibres. The most lateral is the strongest of the three muscles and is attached to the margin of the zygocardiac ossicle (z.c.).

On the side of the cardiac stomach there are six bands of **Lateral Cardiac Muscles** (Fig. 83, l.c.). The two posterior bands are attached dorsally to the external margin of the zygocardiac ossicle (z.c.), while ventrally the more posterior band of the two is attached to the antero-inferior pyloric ossicle (a.i.p.), while the more anterior band is attached to the infero-lateral cardiac ossicle (i.l.). The next four bands are attached to the pterocardiac ossicle (p.tc.) dorsally and to the infero-lateral pyloric ossicle (i.l.) ventrally.

On each side of the cardiac plate are the **Cardiac Constrictor Muscles** (Figs. 83, 84, c.c.m.). They are bisected by the upper anterior dilator muscles (u.a.d.).

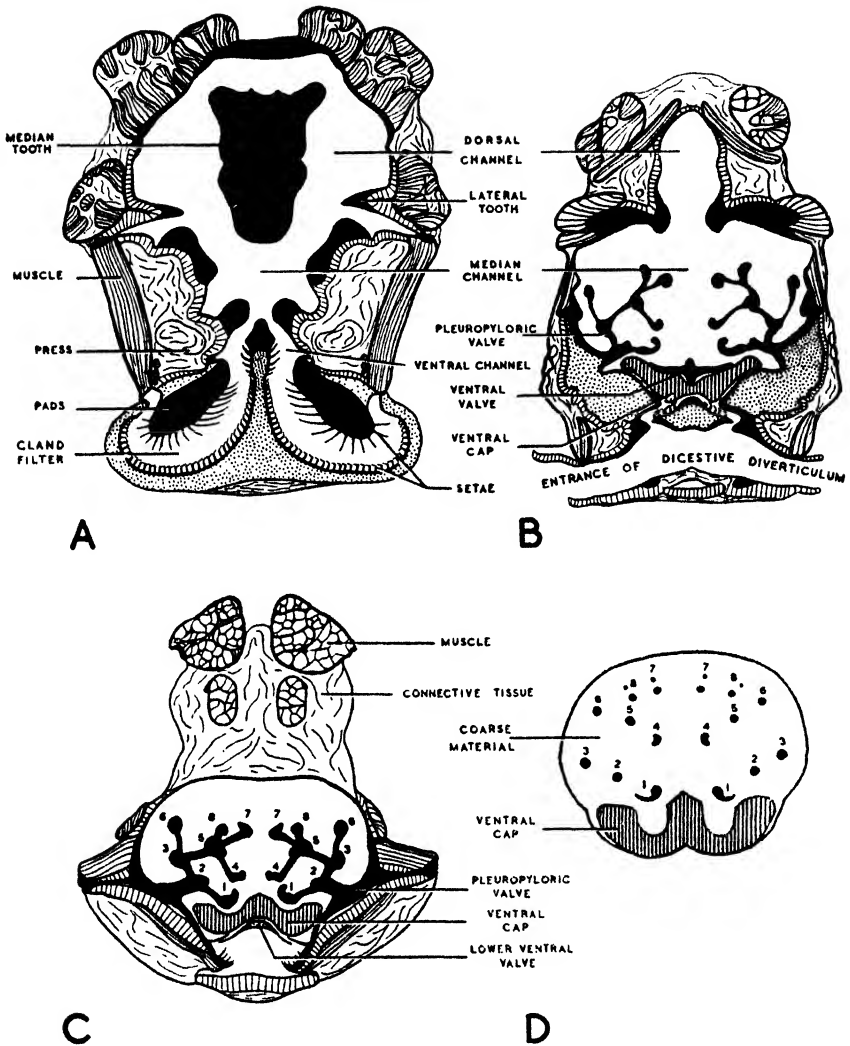
Circular Oesophageal Muscles (Fig. 83, c.o.e.) surround the oesophagus and serve for its constriction.

The side walls of the pyloric stomach support a number of bands of **Lateral Pyloric Muscles** (Fig. 83, l.py.) which have not been differentiated by Mocquard (85). They are mainly attached between the anterior pleuropyloric ossicle (a.pl.) and the mesopyloric ossicles (a.m. p.m.) on the dorsal side and to an extension of the antero-inferior pyloric ossicle on the ventral side.

Three weak bands are also found stretched between the pyloric ampulla and the posterior pleuropyloric ossicle (p.pl.) of each side.

Internal Structure of the Fore-Gut

The internal structure of the cardiac portion of the fore-gut requires little description. It consists of a median tooth (Fig. 82 m.t., Text-Fig. 6 A) lying between, and slightly posterior to, the



TEXT-FIG. 6

A. B. C. Cross sections through the pyloric fore-gut of *Galathea squamifera*.

A. At the level of the hind end of the median tooth and the pyloric filter. It shows the three food channels from the cardiac into the pyloric fore-gut, and the two pyloric filters separated by the median ridge. $\times 10$

B. At the entrance level of the digestive diverticula to show the pleuropylic valves. The fine material of the ventral cap is situated under the ventral valve and above the hinder end of the median ridge. $\times 10$

C. Just posterior to B, showing the single chamber with the pleuropylic valves. The ventral cap is now in the same situation as found in the faecal pellets. $\times 10$

D. Cross section through a faecal pellet of *Galathea squamifera* after Moore (86). The tubular canals running through the faecal pellets are shown in black. $\times 10$

two large lateral teeth (Fig. 82, l.t.). Below the lateral teeth on each side are the lateral accessory teeth (Fig. 82, l.a.t.) and again below these on each side of the oesophagus are the lateral oesophageal valves (Fig. 82, l.o.v.). From these valves arise the post-pectineal ossicles which are closely approached by the infero-lateral cardiac ossicles. Both these ossicles are fringed with close set setae and form the ventral groove from which the coarse material of the cardiac stomach is excluded. This groove allows, however, the secretion of the digestive diverticula from the pyloric stomach to pass forward into the cardiac stomach and the dissolved matter to pass backward.

There is difference of opinion between Huxley (65), Mocquard (85) and Reddy (110), as to the exact way in which the gastric ossicles work. Mocquard's views are more usually accepted because he made his observations when the gastric armature was in action in the living crab, while all alternative views are based on the theoretical mechanical principles involved.

By whatever process the teeth work the result is that the material in the cardiac stomach is ground, mixed, partly digested and the contents passed into the pyloric stomach by one of two routes. The coarse material which consists largely of sand grains, passes each side of the median tooth by either the dorsal or median channel. In *Galathea* these channels are not completely separate as in *Nephrops* (Yonge (131)). The fine material and the dissolved matter from the cardiac stomach pass back by the ventral groove (Fig. 82, vg.) and ventral channel (Text-Fig. 6, A) through the gland filter to the digestive diverticula.

Behind the median tooth, the dorsal and median channels unite into a common median chamber (Text-Fig. 6, C). Posteriorly the lateral walls of the median chamber become thickened and more muscular, forming the structure termed by Jordan (68) the press (Text-Fig. 6, A). Posteriorly the pads of the press are drawn out into complicated Pleuropyloric Valves (Text-Fig. 6, B, C, Fig. 82, pl.v.) ventral to the press, and housed in the ampullae is the pyloric filter or gland filter (Text-Fig. 6, A).

The Gland Filter (Text-Fig. 6, A) consists of two lower

chitinous plates, which, in the median line, unite to form a ridge. The apex of this ridge is produced backwards into a *Ventral Valve* (Fig. 82, v.v., Text-Fig. 6, B), while posteriorly an even longer projection of the ridge forms a *Lower Ventral Valve* (Fig. 82, l.v.v., Text-Fig. 6, C). The lower chitinous plates give rise to a series of chitinous rods bearing stiff setae (Text-Fig. 6, A). These rods are attached to plates along the whole length of the filter chamber. The roof of the chamber bears two semi-circular chitinous pads, from the ventral surface of which further setae project into the filter chamber (Text-Fig. 6, A). Thus the cavity of the filter chamber is screened by two sets of setae forming a very efficient filter through which only the finest material can pass.

The material in the gland filter which has not been dissolved passes backwards and upwards until it comes to rest beneath the ventral valve (Text-Fig. 6, B) and above the posterior end of the ridge. This forms the ventral cap of the faecal pellet. The hind end of the ridge gives rise posteriorly to the lower ventral valve (Text-Fig. 6, C). Below this valve a channel is continued from the digestive diverticula posteriorly until it unites with the hind-gut below the ventral cap.

All particles which do not pass through the gland filter are passed backwards over the ventral valve and between the plates of the pleuropyloric valve (Fig. 82, pl.v., Text-Fig. 6, B, C). These plates project from the walls of the press and grow into a tree-shaped structure (Text-Fig. 6, B, C) beyond which the coarse material must proceed. Moore (86) cut sections through the faecal pellets of different *Anomura* and found that the faeces of some species were divided into a coarse upper and a fine lower layer (Text-Fig. 6, D). The coarse material had longitudinal canals running through the length of the faecal pellets. Moore said that these canals were due to the hardening of the faecal material as it traverses the pleuropyloric plates, but he gave no details concerning the arrangement of these plates. He suggested that the function of the plates might be that of water absorption, but this theory can hardly be supported by the work of Yonge (131). The cross-section of a faecal pellet of *Galathea squamifera* (Text-Fig. 6, D) is taken from Moore's work. It will

be seen that there are eight longitudinal canals arranged in two oblique rows (Text-Fig. 6, D, 1, 2, 3, 4, 5, 6), each side of the median line, with two additional paired dorsal canals (Text-Fig. 6, D, 7, 8). Referring to Text-Fig. 6, C, the cause of these canals is seen to be the thickened portion of the plates of the pleuropyloric valve. These have been numbered in the same way as for Text-Fig. 6, D. Further support of this can be obtained from a photograph by Moore of a cross-section of the faecal pellet of *G. dispersa* where some of the divisions caused by the junctions of the plates with the thickenings are evident.

Comparison of the Fore-Gut, Faecal Pellets and Feeding Methods in the Anomura

The passage of food through the stomach of *Galathea* is essentially the same as that described for *Homarus americanus* by Williams (127) and for *Nephrops norvegicus* by Yonge (131). In both cases the coarse material passes dorsally and the fine material ventrally. In *Galathea*, however, there is no dorsal channel traversing the roof of the pyloric stomach to open into a dorsal caecum, this latter organ being absent. Thus in *Galathea* the food passes only by the median and ventral channels into the hind-gut. In the Galatheidae either the ventral channel carries more material or this material is better separated than in any other Crustacea, as the faecal pellets of this family alone possess a ventral cap of fine material. The median channel, which carries the coarse material, is divided by the plates of the pleuropyloric valve into numerous compartments, which leave their impression on the faecal material. The pattern formed by these plates differs in the various families and is found only in Anomuran pellets (Galatheidea, Thalassinidea and Hippidea). Mocquard (85) noticed that the pleuropyloric valve was composed of five folds in *Galathea*, two in *Grimothea* and a single one, not very noticeable, in *Munida*. Moore (86) points out that the pellets of *Aeglea* are very simple, but yet of a type which can be easily related to that of *Galathea* and *Porcellana*. This is of interest because not only does it indicate relationship between these genera, but also because it allows a comparison between marine and fresh-water species.

The Paguridae and *Munida* are exceptions in that the faecal pellets do not possess canals, but since there are no pleuropyloric valves this is to be expected. In the Thalassinidae the faecal pellets of *Upogebia deltursa* contain a large number of canals and an examination of the pleuropyloric valve shows this to be exceedingly complex and fully capable of producing these canals. There is, however, no ventral cap either in this species or in *Eupagurus*. The presence of a cap is likely to be brought about by difference in internal structure or methods of feeding. There are no evident internal differences capable of producing this cap, nor does the pleuropyloric valve appear to have any direct influence on the fine material.

Moore (86) states that only the detrital feeders possess canals through the faecal material, these being absent in the carnivorous Paguridae and *Munida*, but Orton (92) has shown *Eupagurus* to be mainly a detrital feeder ill-adapted for carnivorous feeding. The detritus is collected by lateral setae on the third maxillipedes; these brush the substratum and pass the collected material towards the mouth, where further sorting is carried out by the other buccal appendages. Nicol (90) has shown that *Porcellana* and *Galathea* eat similar food but the method of collecting differs. In *Porcellana* the third maxillipedes have long bipinnate lateral setae which form an efficient sweep net. The particles caught are combed from the net by the second maxillipedes and passed on to the mouth. The food is therefore composed of fine material, and meat is usually rejected. It was noted, however, that the gastric mill has not decreased in power. The third maxillipede of *Galathea squamifera* (Plate V, Fig. 32) is similar to that of *Porcellana* except that the long bipinnate setae of the sweep net are not so efficient and the terminal setae of the dactylus have been replaced by stiff simple setae among which serrated setae are placed (Fig. 33). This terminal brush acts efficiently as a rake of the substratum, after which the particles are swept to the mouth by the lateral setae and combed out by the second maxillipedes. *Galathea* also appears better adapted for carnivorous feeding than either *Eupagurus* or *Porcellana*. In the deeper water *Galathea dispersa*, the lateral setae become simpler and

shorter, so that they are less suited as sweep nets and better suited as brooms. The setae of the terminal tuft of the dactylus have finer serrations, and both these changes suggest that the habitat is now one of sand rather than inshore boulder conditions. In *Munida* the third maxillipede still more approaches that of *Eupagurus*. It will be noted that this gives a series, viz.:—*Porcellana*—→*G. squamifera*—→*G. dispersa*—→*Munida*—→*Eupagurus*.

Reference to the faecal pellets shows that the ventral cap is largest in *Porcellana*, next largest in *G. squamifera*, small in *G. dispersa* and absent in *Munida* and *Eupagurus*. It is possible that the quantity of fine material eaten is responsible for the ventral cap. This is not supported by *Upogebia pugettensis* which, according to MacGinitie (80) feeds entirely on suspended material. It is also noted that the number of plates on the pleuropyloric valve is the same in *G. dispersa* and *G. squamifera*, but differs in both *Porcellana platycheles* and *P. longicornis*. It appears therefore that neither the food, mode of feeding nor the pleuropyloric valves wholly account for the differences in the faecal pellets in the Anomura.

Further work on this subject might prove profitable, especially if correlated with the food and mode of feeding of *Homarus* and *Palinurus* as opposed to that of the Stenopidae, Penaeidae and Caridae. Patwardhan (97) has pointed out that in these latter three groups the internal masticatory apparatus is either totally absent or so modified as to be in the form of a few denticles. The molar process of the mandibles is much enlarged and chiefly concerned with the grinding of the food into a fine powder.

Hind-Gut

The hind-gut is a narrow tube somewhat flattened on the dorsal side. Anteriorly it is attached to the pyloric fore-gut on the dorsal side and to the mid-gut on the ventral side. From this attachment it passes backwards beneath the pericardial cavity and the posterior end of the reproductive organs to enter the abdomen above the flexor muscles. It then pursues a straight course to the anus where it bends down to the external opening

below the central plate of the telson (Plate VIII, Fig. 54, cent.pl.). No caeca are given off along its length.

As in the fore-gut (*vide* page 48) the hind-gut is lined with a double-layered integument and beneath this is a pronounced columnar epithelium resting on a basement membrane. Outside the basement membrane is a thin layer of circular muscle, while the longitudinal muscle varies from a thin dorsal layer to two thick ventro-lateral bands. On the ventral side of the anterior part of the hind-gut there is a mass of closely-packed tegumental glands, but these thin out in the hinder part.

THE DIGESTIVE DIVERTICULA

The digestive diverticula are composed of masses of tubules forming a large mop-like brownish organ occupying nearly the whole available lateral and ventral thoracic cavities. The tubules are grouped together into four masses on each side (Text-Fig. 5, 1-4, page 49). Each individual tubule communicates with a short collecting duct and this in turn leads into the main collecting tube which opens into the alimentary tract (Text-Fig. 5). The main collecting tube of each side enters the alimentary tract just posterior to the pyloric ampullae and, as previously mentioned, this is the only area of the tract not recognisably lined by chitin.

In transverse section each tubule is composed externally of connective tissue in which a network of fibres and isolated blood sinuses are embedded. Internally an epithelium nearly fills the whole of the lumen of the tubule and consists of two distinct cell types :

1. Absorptive cells (Fat cells, Frenzel (46), Pearson (99)).
2. Gland cells (Ferment cells, Frenzel (46), Pearson (99)).

Histology of the Digestive Diverticula (Plate XIII, Figs. 85-87).

[*Method.*—The whole of the gastric mill with the digestive diverticula attached was removed immediately after death and placed in a fixative. The fixatives employed were : Helly, Bouin, Bouin Dioxan, Gilson and 5 per cent. formalin.

Of these Helly was found to give very satisfactory fixation. Graham (49) and Fretter (47) both found for Mollusca that the appearance of the digestive epithelium varied greatly with the fixative employed and that the chrome-osmic mixtures such as Fleming-without-acetic, Champy or Altmann proved the most satisfactory. The formalin-chrome mixtures of Schridde and Helly also gave comparable results. Contrasted with these, fixatives such as Corrosive sublimate, Bouin Dubosq or Bouin were relatively valueless.

Mallory's triple connective tissue stain proved very suitable for the study of cellular structure. The cytoplasm of the two main types of cell was stained with the acid fuchsin, while the connective tissue, vacuole contents and striated cell borders took up the aniline blue. Weigert's iron haematoxylin counter stained with erythrosin and van Gieson were also employed for staining cytoplasmic granules.]

A cross-section through the distal end of each tubule shows the epithelium thrown into five or six mounds. As the apices of the cells are broader than their bases, the cells on either side of the crest splay out fanwise while the cell between successive mounds is triangular to fill the space that would otherwise occur between two consecutive mounds. The cytoplasm of all these cells is, according to Guieysse (51), striated and the nuclei are regularly situated in the lower third of the cell.

Towards the middle of the tubule differentiation of the cells into two main types occurs, each type being concentrated into two diametrically opposed groups.

The Absorptive Cells (Figs. 85, 87, a.c.) are columnar cells 45μ high and 15μ broad, and their free border is striated. The nuclei are all situated in the basal third of the cell and besides the chromatin one or two prominent nucleoli may be evident. These cells characteristically contain large numbers of fat globules, but some cells containing little or no fat are coarsely granular (Fig. 87, gr.c.) and very evident by their heavy dye absorption. A single vacuole, which may contain an inclusion is sometimes seen above the nucleus, which is slightly larger than in the normal cell. There is little doubt that these granular cells are the same as the striated cells containing little fat seen in *Galathea* by Guieysse (51) and in the Paguridea by Pierre (106). The latter also noticed

that the cytoplasmic striations were lost as the cell became older and took on the normal form of the absorptive cell.

The Gland Cells (Figs. 85, 86, g.c.) are very tall, with the upper half swollen by a large vacuole. They arise from two narrow longitudinal crests, one on each side of the tubule, and their free faces practically meet, end to end, almost obliterating the lumen. The cells are attached to the basement membrane by narrow pedicels, in which the nuclei are situated and surrounded by a small amount of cytoplasm. It is difficult to distinguish which nucleus belongs to which cell as they lie twisted round one another. It is thought that two nuclei are frequently found in a single cell; one is crescent-shaped, opaque and usually attached to the underside of the vacuole, while the other remains at the base of the cell and is similar to that found in the absorptive cells.

Above the nucleus is the swollen vacuole, 140μ high and 25μ broad at its widest part, the contents of which are granular (Fig. 86). Above the vacuole is a strip of vacuolated cytoplasm surmounted by a striated border which is capped by a hyaline layer.

Replacement cells (Figs. 86, rp.c.) are constantly being formed to take the place of old discarded cells. These new cells are not easy to distinguish and are seldom more than half the height of the surrounding cells.

Comparative Morphology of the Digestive Diverticula

There are three types of cells which appear constantly in the digestive diverticula of all decapods :

(a) Absorptive Cells. (b) Gland Cells. (c) Replacement Cells.

There is little difference between the size of the absorptive and gland cells in the *Palinura*, *Astacura* and *Brachyura*, with the possible exception of *Palinurus*, and in no case do the gland cells appear to occupy grouped and segregated positions along the length of the tubules. The replacement cells are similar in all decapods. In the *Anomura* the gland cells differ from the above in both size and location. In *Galathea* they are confined to two narrow crests on opposite sides along almost the entire length of

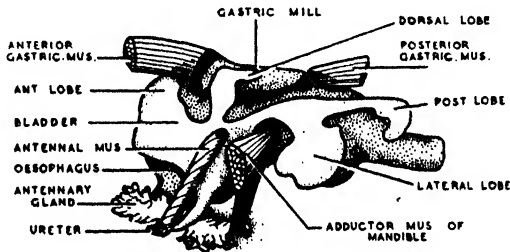
the tubule ; in other Anomura the number of crests bearing these cells varies from one to three, but remains constant within a given species.

In *Dromia* the cell types appear to be similar to those described for the Brachyura.

THE EXCRETORY SYSTEM

Excretion in *Galathea*, as in other decapods, is carried out by three different systems :—

1. The paired Antennary Glands and associated structures.
2. The gland cells of the digestive diverticula (*vide* page 67).
3. The Branchial Excretory System (*vide* page 95).



TEXT-FIG. 7

Lateral view of the excretory system of *Galathea squamifera*. The ureter lies beside the antennal muscle and leads into the antennary gland at the base of the oesophagus. It also leads into the bladder which rises in front of, over and beside the gastric mill. $\times 3$

Of these three systems only the first will be dealt with in this section. The other two systems will be found in the sections dealing with the particular organs.

According to Goodrich (48) and Allen (2), the antennary gland and associated structures are derived from a coelomoduct and are composed of three parts :—

- (a) Antennary Gland [Green Gland, "Rein Antennaire"].
- (b) Bladder. [Vessie (Marchal), Nephro-peritoneal sac (Weldon).]
- (c) Ureter.

Text-Fig. 7 shows the position of these three parts on the left-hand side.

Each antennary gland is a branched, flattened organ situated at the side of the oesophagus and extending in front and behind it. It joins the bladder which consists of a main vesicle giving off four lobes and lies lateral to the gastric mill. The short ureter arises from the junction of the antennary gland and bladder and opens to the exterior by the excretory orifice on the operculum of the antenna.

[*Method.*—To see the bladder remove the carapace from a fresh specimen and the bladder will be found closely applied to the gastric mill and overlying the dorsal surface of the digestive diverticula. By cutting through the oesophagus the gastric mill can be removed together with the digestive diverticula, and the antennary glands will then be seen lying on the floor of the thorax on each side of the oesophagus. This will be more clearly seen if intravital stains have previously been injected into the body cavity (vide histology of end sac., page 70).]

The Antennary Gland (Plate XIV, Figs. 89-94).

Marchal (81) made a careful and accurate study of this organ in *G. strigosa* and this work on *G. squamifera* has confirmed Marchal's findings in all essentials. He states that the antennary gland of *G. strigosa* presents a peculiar arrangement which has only been met with previously in *Porcellana*. It appears therefore that although in the Galatheidae the antennary gland differs in form from the rest of the Anomura, as well as from that of other decapods, it retains the essential elements and occupies a similar position. It is to be found resting on the sterna of the cephalon anterior to the mandibles and on each side of the oesophagus. It thus forms a bed upon which the cardiac fore-gut rests. The organ is divided into lobes which are again subdivided into smaller lobes. All the lobes converge on the point of origin at the Hilum (Fig. 91, hil.) which is situated close to the muscle of the antenna. Anterior to the oesophagus the smaller lobes of the gland interlace in the median line with those of the gland of the opposite side, but no fusion or cross-connection takes place. The whole gland rests quite freely on the sterna and is only connected with other tissue at the hilum.

The antennary gland is made up of two portions :—

- (a) End sac (Saccule of Marchal).
- (b) Labyrinth.

In most decapods the end sac is a small dorsal portion which gives off ventral prolongations, while the labyrinth is ventral and closely applied to the end sac. In *Galathea* the end sac is similar in form and size to the labyrinth by which it is completely surrounded, and in which it is embedded.

The End Sac (Figs. 91-94).

The End Sac (Figs. 91, 92, e.s.) consists of a series of ramifying branches radiating outwards from the hilum (Fig. 91, hil.) almost to the extremities of the smaller lobes (Fig. 92, black.). Each lobe of the antennary gland thus consists of an end-sac axis embedded in the network of the labyrinth. This arrangement of ramifications (Fig. 92) is clearly shown after injection of intra-vital basic dyes into the body cavity of the animal.

Histology of the End Sac (Figs. 93, 94, e.s.)

[*Method.*—Cuénot (30) found that the cells of the end sac have an acid reaction and eliminate such substances as methyl green and ammonium carminate when these are injected into the body cavity. Both these substances were found to be eliminated by the end sac in *Galathea*. In addition, certain weakly acid dyes such as trypan red, trypan blue and bismarck brown were also eliminated. Cuénot states that bismarck brown is eliminated by the alkaline cells of the labyrinths.

Intra-vital stains were injected into the body cavity of the living animal. Two injections a day for two or three days were given of approximately 0.5 c.c. of fluid of 0.5 per cent. solution in sea water, after which the glands were dissected out and fixed in Gieson's fluid, or 10 per cent. formalin.

For a general view whole mounts were made by simple clearing and mounting in Balsam.

To find the relationship between the tissue of the end sac and labyrinth material stained intra-vitam and fixed in Gieson's fluid was embedded and sectioned. The sections were subsequently stained

with haemalum (Mayer) without differentiation in acid alcohol. It was previously noted that even weak acid solutions caused bleaching of the intra-vital dyes. For cellular detail, further sections were stained with Mallory's triple stain and also Weigert's iron haematoxylin. As a counter stain to the latter both van Gieson (picro-säurefuchsin) and erythrosin were used.]

In section the end sac is clearly shown to be suspended between an upper and lower layer of labyrinth (Figs. 93, 94, e.s.). It is held in position and attached to the labyrinth by narrow strands each formed by a prolongation of a cell of the end sac. The cells of the end sac are ovate (12μ), thin walled and loosely applied to each other. The cellular cytoplasm is finely granular, with a large centrally placed nucleus. The cells on their inner free border are frequently swollen and contain vacuoles with granulated centres (Fig. 94, v.c.).

The black material shown towards the base of the end sac cells in Fig. 94 is injected ammonium carminate.

The lumen of the end sac is found to be full of degenerating cells in varying stages of decomposition. Those most recently cast off (Fig. 94, c.c.) still possess a nucleus and ingested particles of carmine.

The Labyrinth (Figs. 90, 92-94).

The Labyrinth (Figs. 90, 92, lab.) is a reticulated envelope surrounding the ramifications of the end sac. This reticulated appearance is clearly brought out with intra-vital indigo carmine (Fig. 90). If at the same time ammonium carminate is injected into the body cavity to stain the end sac, then it will be seen that the labyrinth is two layered, one layer above and another below the end sac, the two layers merging beyond the limits of the latter (Fig. 92). Marchal (81) states that in *G. strigosa* the thickness of the upper layer is double that of the lower. In *G. squamifera* the upper layer (Fig. 93, lab.u.) is certainly thicker than, but seldom double that of the lower (Fig. 93, lab.l.). The reticulated appearance (Figs. 90, 92, 93) is produced by the lumen of the labyrinth being divided by cross connections. Near the junctions with the end sac the labyrinth cross-connections become less

numerous and at the hilum communication with the bladder takes place. Connection is not established with the actual body of the bladder, but with the vesicle canal close to its exit (Fig. 93, ves.c.). It is at this point only that the gland adheres to the bladder.

Histology of the Labyrinth (Figs. 93, 94, lab.u., lab.l.)

As already stated, there are two parts, one above and one below the end sac. Each part consists of an upper and lower layer surrounding the lumen of the labyrinth.

The cells of the upper layer above the end sac ramifications (Fig. 94, lab.u.) are approximately 50μ tall, and the majority are topped by a clear vesicle (Fig. 94, c.v.). Below the vesicle the cytoplasm is granular with a fibrous tendency and with the nucleus situated towards the base, where inclusions may also be seen.

According to Fischer (44) the cytoplasm is striated, the striae being more pronounced towards the base, and produced by strands of granular and non-granular cytoplasm. Some authors have stated, however, that the granular cytoplasm is interspersed by vacuolated strands, thus giving the effect of striations.

In *G. squamifera*, as already stated, the cytoplasm is granular and tends to be fibrous, especially towards the base of the cell, but a definite striation is not evident.

Marchal (81) also states that the borders of the cells have a cuticular appearance but are not striated in *G. squamifera*. Fischer (44) believes that the cells in this species are surmounted by a striated cuticle. This belief is based upon differential staining reactions. Striated borders (Fig. 94, st.br.) have been seen on a number of these cells, but the cuticular nature of the border could not be determined with certainty.

The cells of the lower layer of the same part are generally shorter than in the upper layer (approx. 37μ) but this is not constant. In places the nuclei are congested and the epithelium has an appearance of pseudo-stratification (Fig. 94, ps.c.).

The cells of the layer below the end sac (Fig. 94, lab.l.) are more flattened (26μ) and are not topped by vesicles. Frequently also the upper layer of cells are shorter than the lower (Fig. 94, lab.l.).

As in the end sac, the lumen of the labyrinth is filled with degenerating cells (Fig. 94, c.c.) containing excreted material. When excretion has been excessively heavy, whole rows of labyrinth cells will be found in a state of active division, or with resting nuclei. In this state the nucleus stains bright red with Mallory's connective tissue stain, and lacks reticulation when other stains are used (Fig. 94, r.n.).

The Bladder (Plate XIV, Figs. 88, 91, 93).

The Bladder (Fig. 88, bl., Text-Fig. 7) is formed of a single layer of cells having a white appearance in the fresh specimen. In the centre it is partially constricted by the adductor muscle of the mandible into anterior and posterior portions.

The main vesicle (Fig. 88, bl.) arises from the hilum and is closely applied to the stomach. Two lobes are given off, one passing in front of the stomach and below the anterior gastric muscle (Fig. 88, a.g.m.), the other, given off from the dorsal part of the main vesicle, passes above the cardiac fore-gut (Fig. 88, bl. 2). Both lobes meet, but do not join, the corresponding lobes arising from the bladder of the opposite side.

Posterior to the constriction caused by the adductor muscle of the mandible, two more lobes of the bladder overlies the anterior portion of the digestive diverticula. One lobe keeps close to the pyloric stomach (Fig. 88, bl. 4), the other passes laterally and makes contact along its anterior edge with the adductor muscle of the mandible, continuing beside the apophysis of the mandible until nearly reaching the antennary gland (Fig. 88, bl.3).

Histology of Bladder (Fig. 93)

The bladder epithelium is one cell thick, with cells similar to those found in the labyrinth but less tall. There are no vesicles in the cells, and in species with colourless bladders there are no inclusions.

The Ureter (Plate XIV, Fig. 93).

The Ureter (Fig. 93, ur.) passes downwards and ends at the excretory tubercle. Throughout its course and especially in the last part, numerous short caeca are present.

Blood Supply to the Antennary Gland (Fig. 9I, r.a.)

Blood is supplied to the antennary gland by the Renal Artery (Fig. 9I, r.a.). This is a branch of the antennary artery from which it originates just before the antennary and antennular branches. The gland receives the renal artery on its lower surface at the level of the hilum. On entering the gland it forms a small sinus in the origin of the hilum, and then divides into two or three small vessels. These vessels according to Marchal (8I) form the origin of a fine network of capillaries surrounding all the ramifications of the end sac and separated from the reticulated sheath of the labyrinth. In *G. squamifera* this has not been observed, owing to imperfect injection. There is little doubt however that a condition similar to that found in *G. strigosa* exists. Marchal also states that the blood leaves the gland by small sinuses situated in the cross connections of the labyrinth, subsequently returning to the general circulation.

Comparative Morphology of Antennary Glands and Associated Structures

There is great diversity within the tribes and in consequence it is difficult to obtain a clear picture.

In the Anomura the antennary gland of *Galathea*, *Munida* and *Porcellana* have similar characteristics, but there is considerable difference in size and extent of the bladder. According to Marchal (8I) the bladder of *Porcellana* is reduced to the vesicle canal. In *G. strigosa* there are two main lobes, whilst in *G. squamifera* these two lobes are sub-divided to give four lobes. In the Paguridea the bladder reaches its greatest complexity, while in the Thalassinidea (which appear more nearly related to the Paguridea than the Galatheidea) the bladder is again reduced to a small anterior part of the gland.

Although in the Anomura (Galatheidea, Paguridea, Thalassinidea) the appearance, shape and size relationship of the parts are inconsistent, certain anatomical characters appear to be constant.

- (i) The end sac is embedded in and surrounded by the labyrinth.

- (ii) The blood supply to the antennary gland is by the renal artery only.

In the tribes Palinura and Astacura as represented by *Palinurus vulgaris* and *Homarus vulgaris*, the bladder is a simple vesicle, and the antennary glands present a quite different appearance.

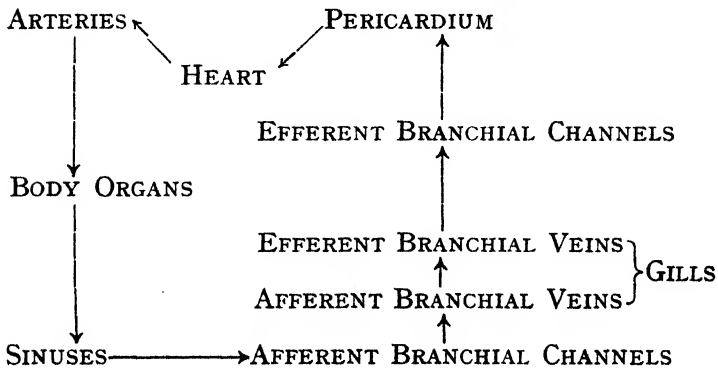
In the Brachyura there does not appear to be so much divergence from type. The bladder consists of three main lobes and this is constant throughout the group. Differences which do occur may be correlated with change in shape of the carapace. *Dromia* (Marchal (81), Bouvier (19)) appears to be an exception for the bladder in this genus rivals *Pagurus* in the extent of its ramifications, while the gland appears to be more Brachyuran than Anomuran in character.

The following characters appear to be constant for the Astacura and Brachyura, but exceptions may be found in the Palinura.

- (i) The end sac is situated dorsal to the labyrinth and in contact with it only on the ventral side and at the margins.
- (ii) The blood supply to the antennary gland is by both the renal artery and by the anterior prolongation of the ventral thoracic artery.

BLOOD VASCULAR SYSTEM

A schematic circulatory system is shown below.



Heart (Plate XV, XVI ; Figs. 95, 96, 98, 99, h.t.)

The heart lies in the pericardial cavity, enclosed by a thin membrane, and is situated immediately beneath the cardiac region of the carapace and above the hind-gut. The heart is flattened dorso-ventrally and when viewed from above is pear-shaped with a narrow anterior end. It is suspended in the pericardial cavity by strands of connective tissue termed the *alae cordis*. In *Galathea* these are rather diffuse and difficult to distinguish. The main lateral suspensions are :—

- (a) Two anterior bands near the antennary arteries.
- (b) Two broad lateral bands at the widest part of the heart and attached to the lateral walls of the pericardium.
(This broad suspension may be divided in two).
- (c) Posteriorly there are three bands, one median and two postero-lateral suspensions.
- (d) Ventrally there are one or two bands attached to the ventro-lateral border of the heart and to the ventro-lateral pericardial walls.

The blood enters the heart by means of three pairs of ostia, two lateral and one ventral. The lateral ostia are situated one on each side of the lateral *alae cordis*, whilst the ventral pair are much smaller and situated just posterior to the hepatic arteries.

Histology of the Heart (Plate XVI, Figs. 98, 99)

[*Method.*—Fresh hearts were dissected out and fixed immediately in Zenker formol, embedded and sectioned serially at 8 μ .

One series was stained with Verhoeff's elastic tissue stain (McClung), and counter stained with erythrosin, no elastic fibres were identified.]

Histologically the heart consists of an outermost layer of connective tissue fibres beneath which rests a broad layer of cushion endothelium from six to twelve cells deep. The cells are irregular in shape with clearly marked boundaries and centrally placed spherical nuclei. The cell cytoplasm is non-granular. At the inner edge of the endothelial layer the cells become more flattened and tightly packed into two or three layers. These cells are heavily granular. Arising from this inner cell layer

muscle fibres traverse the lumen of the heart in all directions. In transverse sections the cut ends of groups of muscle fibres traverse the heart antero-posteriorly, these however are mostly located near the periphery of the lumen. Between the muscle fibres, cavities of varying size are present in which may be seen cellular elements of the blood. The bundles of muscle fibres present a striped appearance similar to that seen in normal body muscle. The nuclei in the muscle fibres are flattened and oval in shape.

Ostia

Blood is prevented from returning into the pericardial cavity by means of the ostial valves. The valvular mechanism appears to consist of a simple aperture on the inner surface of which are two strong oblique muscles (Fig. 99, o.m.h.). The thick endothelial wall ends abruptly on each side of the ostium to form outwardly a distinct concave pit. The floor of this pit consists of a thin layer of epithelial cells continuous and identifiable with the layer of cells surrounding the rest of the lumen (see above description). These cells seem to form two projecting lips meeting in the centre of the pit. On their inner surface are strong muscle attachments passing obliquely to their connections at the base of the pit (Fig. 99, o.m.h.). From the observed structure it is suggested that at diastole when all the cardiac muscles are relaxed the ostium is open. At systole the oblique ostial muscles will contract and draw the lips together and downwards, whilst the endothelial ridges will move towards each other thus further sealing the aperture.

This mechanism does not appear to be the same as that found in the lobster *Homarus* (Herrick (63)), where each ostium is provided with valves which open inwards, so that the blood once admitted to the heart cannot be regurgitated into the pericardial sinus. In *Astacus* a similar mechanism to that of *Homarus* appears to be present.

Arterial Valves (Fig. 98)

Under systolic pressure blood is forced into the arteries. During diastole blood is prevented from returning to the heart by means of valves situated immediately beyond the junction of the vessel

with the heart. These valves are conical in shape with the apex of the cone projecting into the lumen of the vessel and away from the heart cavity (Fig. 98, a.v.). Approximately on the level of the inner wall of the heart the endothelium becomes thin and divides, one side continuing to form the inner margin of the vessel and the other forming the projection of the valve. The endothelial layer of the valve is two or three cells thick. On the innermost margin of the valve thin slips of striped muscle are closely attached and continuous from the conical apex of the valve to the wall of the heart cavity.

Bouvier (21) illustrates a valvular mechanism for *Astacus* and *Palinurus*, consisting of two semi-circular valves. This gives a picture similar to that here described for *Galathea*.

The wall of the vessels consists solely of a membrane upon which rests a simple compact layer of cells each possessing a spherical nucleus.

The Arterial System (Plate XV, Figs. 95-97)

[*Method.*—Owing to the thin nature of the vessels it is impossible to dissect more than the main trunks without previously injecting the system. Delage (33), in 1881, found that lead chromate was very satisfactory. This method differs slightly from that used by Milne-Edwards (83). Two parts of lead subacetate (basic lead acetate) are poured into a vessel containing one part of potassium bichromate and the whole is shaken vigorously. A light yellow precipitate results and this constitutes the injection mass without further addition or dilution. Used in this way Delage found that it had good penetration without reaching the sinuses. For the present work indian ink (Higgins or Pelican) was found to make a very satisfactory injection medium, the black showing up well against the white of the muscle. With larger animals such as *Munida*, indian ink is too penetrating and enters the sinuses. For such animals liquid latex "T" thinned with ammoniated distilled water, and suitably coloured gives an excellent injection mass. It is difficult to use with *Galathea* as the viscosity of the latex makes penetration of the finest arterioles almost impossible. In each case a fine glass cannula was inserted directly into the heart, the overlying

portion of the carapace having been previously removed. When using latex, care must be taken to keep the cannula away from acid. Any acid which may be present causes setting of the latex, hence the dilution of the latex with ammoniated water. After injection with latex the animal is placed in formalin to which a little acetic acid has been added.]

THE ARTERIES (Figs. 95-97)

There is no general agreement concerning the names applied to the arteries. H. Milne-Edwards (83) and Bouvier (21) appear to be the most prominent of the early authors, but subsequent writers have not always retained the names they gave. In the present work the names which appear to be most appropriate have been selected.

Five arteries arise from the anterior end of the heart, one median and two pairs laterally. These are termed :—

1. Median Cephalic (Ophthalmic of Bouvier).
2. Antennary (Lateral *aucts.*).
3. Hepatic.

From the posterior end of the heart two arteries leave from a common aperture.

4. Dorsal Abdominal (Superior Abdominal, Bouvier).
5. Sternal (Descending Artery, *aucts.*).

The sternal artery subsequently divides into :—

6. Ventral Thoracic (Maxillipede, Bouvier).
7. Ventral Abdominal (Inferior Abdominal, Bouvier).

In *Galathea squamifera* the dorsal abdominal artery is represented by two lateral arteries lying one each side of the hind-gut. The sternal artery, after passing through the ventral nerve cord, supplies the thoracic legs, the mouth appendages, the labrum and the oesophagus. This forward extension of the sternal artery was termed by Bouvier the maxillipede artery, but in the present work it will be referred to as the ventral thoracic artery ; while its posterior ventral prolongation into the abdomen will be termed the ventral abdominal artery.

The Median Cephalic Artery (Figs. 95, 96, m.c.a.) is a slender vessel passing forwards above the gastric mill and

descending through the anterior gastric muscles to open into two lacunae within the supra-oesophageal ganglion. On its descent to the supra-oesophageal ganglion it passes through a small pocket of tissue surrounding the stomatogastric ganglion (*vide* Lymphatic glands, page 87). It is thought to supply this pocket with blood. Just before entering the supra-oesophageal ganglion two branches are given off which unite in the median line within the rostrum, and also two small branches which penetrate the ocular peduncles on their mesial faces.

On each side of the median cephalic artery arise the Antennary Arteries (Figs. 95, 96, a.a.). They are also dorsally situated and pass forwards under the carapace to the antenna of each side. From each antennary artery a lateral branch is given off to supply the lateral cardiac muscles of the fore-gut (Figs. 95, 96, right-hand side). This lateral branch also sends smaller branches over the cardiac fore-gut which finally run into the cleft between the zygo-cardiac ossicles (*vide* Lymphatic glands, page 87). From the antennary artery also, branches are given off to supply the integument, gonads and bladder of the antennary gland (Fig. 96, left-hand side). Just before the artery dips ventrally to supply the antenna and antennary gland, three branches, two posterior and one anterior, are given off. One of the posterior branches continues to the integument of the pleural fold (Fig. 96, right-hand side), whilst the other offshoot passes ventrally to supply the mandibles and in doing so passes down the centre of the external adductor muscle of the mandibles. This muscle is attached ventrally to the mandible and dorsally to the carapace. The anterior branches pass forwards to supply the antenna, antennules, antennary gland and eye, while a forward prolongation passes to the rostrum and sends off a few lateral branches to the anterior gastric muscles. The artery to the eye enters the peduncle on the postero-lateral side and is about twice the diameter of the branch from the median cephalic artery previously mentioned. The antennary supply to the rostrum is also larger than that of the cephalic arterial supply and penetrates the rostrum laterally after passing dorsal to the eye peduncle

along the internal edge of the carapace. The rostrum is therefore supplied by three arteries, two lateral and one median.

Hepatic Arteries (Figs. 95, 96, h.a.) descend to ramify in the digestive diverticula of each side. Each gives off a branch to the ventral surface of the pyloric fore-gut.

From the posterior end of the heart a single trunk is given off, which immediately divides into three branches. In *G. squamifera* this junction is all that remains of the dorsal abdominal artery. In other Anomura this artery is well developed (see Text-Fig. 8). The two lateral branches pass one each side of the hind-gut and have been termed here the **Latero-dorsal Arteries** (Figs. 95, 96, l.d.a.), while the other branch is ventral and is termed the **sternal artery** (Figs. 95, 96, s.a.). Each latero-dorsal artery gives off a forward branch to supply the thoracic portion of the abdominal flexor and extensor muscles and the posterior portion of the carapace. Bouvier (21) termed this branch the **Posterior Lateral Artery** (Fig. 96, p.l.a.). In *Galathea squamifera* this artery does not appear so pronounced as in some other Decapoda. Segmental branches are given off along the course of the latero-dorsal arteries to supply the pleopods (Fig. 95), while the posterior extremity sends branches to the uropods and telson. Fine median branches lying between the extensor and flexor muscles are given off to supply the lateral walls of the hind-gut (Fig. 96, left-hand side). Further branches from the latero-dorsal arteries supply blood to the extensor and flexor muscles of the abdomen.

The **Sternal Artery** (Fig. 95, s.a.) arises from the same junction as the latero-dorsal artery and descends on the right-hand side of the hind-gut. At the level of the hind-gut, branches are given off which supply the reproductive organs and the posterior part of the digestive diverticula. The sternal artery then passes forwards and under the thoracic endophragmal bridge (Fig. 95, t.b.) to perforate the ventral nerve cord between the ganglia supplying the third and fourth pereopods. Ventral to the nerve cord the artery divides, giving rise to anterior and posterior branches. The anterior branch is termed the **Ventral Thoracic Artery** (Figs. 95, 96, v.th.a.) and the posterior branch entering

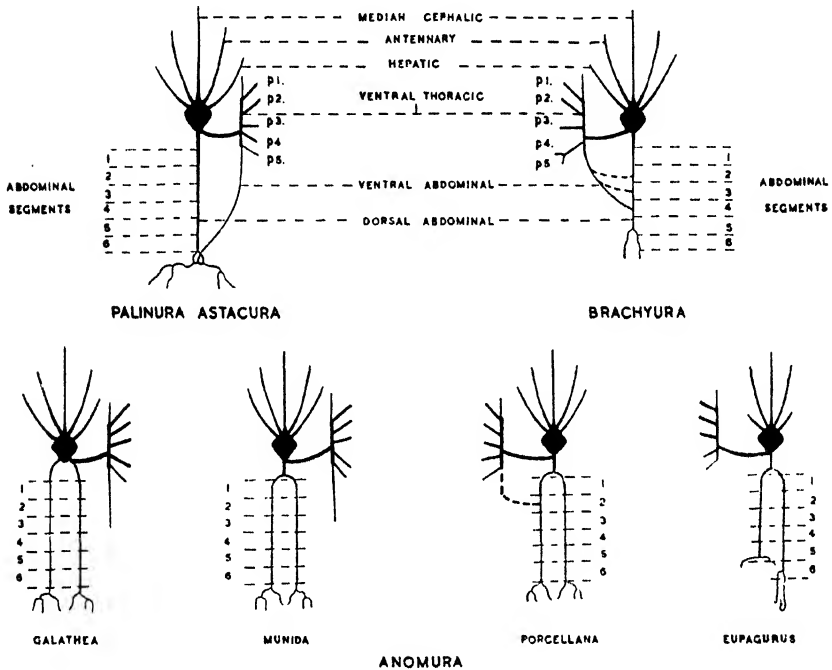
the abdomen the **Ventral Abdominal Artery** (Figs. 95, 97, v.a.a.). The ventral thoracic artery gives off branches to the pereopods, the maxillipedes, the maxillae, the labrum and the oesophagus. The oesophagus and labrum are supplied from the median anterior prolongation of the main trunk, while the anterior thoracic appendages are supplied from two anterior lateral trunks.

The ventral abdominal artery is a thin median artery passing along the ventral side of the abdomen below the ventral nerve cord. Branches are given off in somites 13-18, which pass dorsally round the nerve cord to supply the ventral surface of the hind-gut. The largest is an unpaired branch opposite the fifth pereopod. No connection with the two latero-dorsal arteries has been found from this or other branches of the ventral abdominal artery.

Comparative Morphology of the Arterial System

The median cephalic artery is more developed in both the *Astacura* and *Brachyura* than in the *Anomura*. In many *Brachyura* this artery, together with the antennary artery, supplies the eyes and antennae. The antennary artery, however, is chiefly responsible in all decapods for supplying the anterior cephalic appendages, the walls of the fore-gut, the antennary gland and the carapace. Some of the *Astacura* possess a ventral connection between the cephalic artery and the anterior thoracic artery. The hepatic artery differs little in the decapods except in the *Anomura* (*Paguridae*, *Thallassinidae*), where the digestive diverticula have been largely displaced into the abdomen. The ventral thoracic arteries also differ little in the various groups. In the *Oxyrhynchidae* the connection between the ventral thoracic artery and the sternal artery is not effected through the ventral nerve cord. Here, the sternal artery passes behind the thoracic ganglionic mass, thus allowing a maximum concentration of the nervous system. In all decapods the supply of the last two pereopods takes place posterior to the junction of the ventral thoracic and sternal arteries. In *Galathea* this supply may be separate (Fig. 97), or may arise from a common trunk (Fig. 95). At the junction of the sternal artery

with the heart and the dorsal abdominal artery there is some variation. In the Astacura the sternal vessel appears to arise from the dorsal abdominal artery, while in the Brachyura it originates directly from the heart. In *Galathea* the point of origin of the sternal artery from the heart is the same as that for the latero-dorsal arteries. The great difference in size of the



TEXT-FIG. 8

Schematic arterial systems of various Decapoda.

In the Brachyura the dotted lines between the ventral and dorsal abdominal vessels indicate possible variations in position of the junction.

In *Porcellana* this connection is dotted because although figured by Bouvier (21) it has not been confirmed by the present author.

abdomen between the Astacura on one hand and the Brachyura on the other has led to the greatest variation in the abdominal arteries. In the Astacura, Palinura and Brachyura there is one main dorsal and one ventral abdominal artery (Text-Fig. 8). In the Astacura and Palinura the dorsal vessel is always the larger, but in the Brachyura there is a gradual change over from

Grapsus—→*Portunus*—→*Carcinus* until in *Maia* the position is reversed and the ventral artery is larger. Connection between the dorsal and ventral arteries takes place behind the peri-intestinal ring of the sixth segment in most Astacura. In the Brachyura, although there is a peri-intestinal ring, connection with the ventral artery is usually effected further forward. In *Grapsus* this takes place in the fifth abdominal segment, in *Cancer* in the third segment, and in *Corystes*, *Carcinus* and *Portunus* in the second segment.

In the Anomura, Bouvier (21) found in *Porcellana* that the dorsal abdominal artery divided into two lateral branches before entering the abdomen. The ventral abdominal artery, although much thinner than the dorsal artery, makes numerous connections with the latero-dorsal arteries. The connection of greatest importance takes place in the second abdominal segment. In *Porcellana platycheles*, where indian ink injections appear to have been complete, no ventral abdominal artery has been observed by the present author. In another paper written in the same year, Bouvier (20) described, but did not figure, the blood system of *Galathea squamifera*. He stated that the dorsal abdominal artery bifurcates soon after leaving the heart, but whilst still within the thorax. This would give an appearance identical with that found in *Porcellana*. In a third paper, Bouvier (18) did not confirm this point. It will be seen, however, in Figs. 95, 96, and in Text-Fig. 8, that the bifurcation takes place immediately in *Galathea*, whilst in *Porcellana* the dorsal abdominal artery runs for a short distance before bifurcating into the two latero-dorsal arteries. *Porcellana* and *Munida* are identical in this respect. In his main paper, Bouvier (21) said that this arrangement was due to the dorso-lateral depression of the abdomen which displaced the more usual posterior bifurcation forward to the thoracic position. No cause was assigned to the condition observed in *Galathea*, nor can the above argument hold for such a condition. The weak ventral abdominal artery with its lack of distinct connections with the latero-dorsal arteries was, however, observed by Bouvier (20). It seems somewhat surprising, therefore, that he should find the ventral abdominal artery so

relatively strong in *Porcellana*, while it is weak in *Galathea* and *Gebia* and absent in *Eupagurus*.

To complete the Anomuran picture it is necessary to glance at the conditions observed in the Paguridae and Thalassinidae. Text-Fig. 8 shows the condition in *Eupagurus* (*Gebia* is not figured). In *Eupagurus* the dorsal abdominal artery divides into two at about the same level as in *Porcellana*. The left abdominal branch remains in the dorsal position, while the right branch passes ventrally to supply the ventral muscle bed, the hind-gut and the terminal portion of the abdomen. In *Gebia* the bifurcation does not take place until the fifth abdominal segment, when the right-hand branch descends to the ventral side as in *Eupagurus*. The ventral abdominal artery in *Gebia* terminates at the fourth abdominal segment.

It is suggested therefore that the bifurcation of the dorsal abdominal artery which takes place in the Anomura is a characteristic feature of the tribe and shows a close inter-relationship of the families.

In the Anomura there appear to be two main groups, the Galatheidea on the one hand and the Thalassinidea and Paguridea on the other (the author has not been able to examine the Hippidea). The position of *Dromia*, as usual, remains doubtful. A short paper by Bouvier (19) gives a brief description without a figure of the blood system, and it appears to be not unlike that of *Porcellana* with the latero-dorsal bifurcation taking place at the fourth abdominal segment.

Blood Sinuses and Blood Channels (Plate XVI, Figs. 100, 104)

[*Method.*—The blood lacunae were filled by the injection of coloured liquid latex "T" into the ventral sinus. This was then hardened in 10 per cent. formalin, to which a small amount of acetic acid had been added. The integument was then decalcified in 30 per cent. sodium hexametaphosphate for six days. Parts of the carapace and sternal abdominal chitin were removed to allow the penetration of gelatin for embedding. After embedding the gelatin was hardened in formalin and coarse hand sections cut to show the distribution of the sinuses.

The efferent branchial channels and pericardial pouches were filled with latex by injection into the pericardial cavity.]

THE BLOOD SINUSES (Fig. 100, 104)

The blood supplied by the arteries to the various organs of the body does not pass to the gills for oxidation along definite channels, but flows through an irregular network of haemocoelic lacunae, or sinuses. These lacunae are all inter-connected and might therefore be considered as one large sinus, although there is a rough division into dorsal and ventral portions. Blood from these sinuses eventually enters the ventral thoracic sinus and passes through the gills and back to the pericardium.

In the thorax the main sinus is the *V e n t r a l T h o r a c i c Sinus* (Fig. 104, v.s.). This sinus is not clearly delineated, but is situated below the thoracic endophragmal bridge (Fig. 95, t.b.) and receives blood from the sinuses of the anterior part of the thorax, the head and the abdomen.

Anterior to the ventral thoracic sinus the main sinus is large and situated above the lateral lobes of the bladder and it extends dorsally above the cardiac portion of the gastric mill. Extensions also pass down each side of the cardiac fore-gut and join the ventral thoracic sinus behind the oesophagus. Posteriorly there are two abdominal sinuses, one dorsal and the other ventral, of which the latter continues directly into the ventral thoracic sinus. The dorsal abdominal sinus surrounds the alimentary canal and makes contact with the ventral thoracic sinus just posterior to the heart.

From the ventral thoracic sinus the blood is carried to the gills by the *A f f e r e n t B r a n c h i a l C h a n n e l s* (Fig. 104, a.b.c.). The main difference between this system and that of *Cancer*, is that in *Cancer* the afferent branchial channels pass down the pleural muscle chambers to the gill bases, while in *Galathea* they rise upwards to reach the gills from the bases of the pereopods.

The blood passes from the afferent branchial channels to the *A f f e r e n t B r a n c h i a l V e i n s* of the branchiae (Text-Fig. 9, A, C, v.a.), through the branchial lamellae to the *E f f e r e n t*

Branchial Veins (Text-Fig. 9, A, C, v.e.) and from there by way of the Efferent Branchial Channels (Figs. 100, 104, e.b.c.) to the pericardial cavity. The first efferent branchial channel is formed by the union of branches from the third maxilliped and the first pereopod (Chela). Pereiopods two, three and four each have their own channels which unite just before entering the pericardial cavity (Fig. 100). Pereiopod five has a separate channel with its entrance at the posterior end of the pericardial sinus.

Pericardial Pouches

Cuénot (30) noticed and described the pericardial pouches found in some decapods, including *Galathea*.

In the Brachyura these pouches are found on each side of the pericardium. They overlie the branchial cavity and continue posteriorly as far as the abdomen. The pouch is traversed by muscle fibres which, on contraction, force the blood into the pericardium.

In the Anomura (*Galathea*, *Eupagurus*) and in the Palinuridae the pouches are reduced and modified to form two diverticula arising from the posterior angle of the pericardium.

There does not appear to be anything comparable with this in the Astacura.

The pouches are clearly seen after injecting the pericardial cavity with latex "T" (*vide* page 86).

Lymphatic Glands

In the Palaemonidae, Weldon (125) and Allen (2), noticed at the anterior end of the median cephalic artery a small mass of cellular tissue which according to them, probably formed blood cells. Guided by this information, Cuénot (30) found what he considered to be lymphatic glands in decapods. In the crayfish this gland covers the whole of the dorsal surface of the cardiac stomach, bounded anteriorly and posteriorly by the anterior and posterior gastric muscles and laterally by the zygocardiac ossicles. Arteries branching from the antennary artery and supplying the stomach ramify on its dorsal surface. These arteries in *Galathea* (*vide* page 80, and Fig. 96),

converge to a central point between the zygo-cardiac ossicles (Fig. 80, z.c.) and serial sections through this area suggests that a cellular aggregation surrounds this convergence. It is possible that this might be a lymphatic gland.

In *Galathea* the stomatogastric ganglion (*vide* page 97 and Plate XVII, Fig. 107, s.g.) is also surrounded by a loose covering of cells through which the median cephalic artery passes and which it is thought to supply. In sections cut through this region, the artery is seen to be surrounded by a dense mass of nuclei somewhat similar to those surrounding the optic centres and the supra-oesophageal ganglion, but these do not make contact with it. It is thought that further investigation might prove these cells to be the median frontal organ observed by Hanström (56, 57, 58) in a somewhat similar position in prawns. He states that in decapods other than the Natantia the organ is usually absent and was not observed in either the Palinura or the Astacura. In the Anomura, however, although absent in *Munida* and *Porcellana*, the organ was observed in *Emerita analoga*, where it formed a well-developed unpaired mass but not a typical median frontal organ.

RESPIRATORY SYSTEM

The branchiae or gills are situated within the branchial chamber on each side. The inner wall of the chamber is formed by the thoracic epimera. The gills arise (Arthrobranchs and Pleurobranchs) from the epimera and from the arthrodial membrane joining the epimera and the legs. The outer wall of the branchial chamber is formed by the down-growth of the carapace, the pleural fold. This enclosure of the branchial cavity is less complete than in the Brachyura. Zimmerman (136) states that the shape of the branchial cavity in *Galathea* is intermediate between that of *Homarus* and *Cancer*. The three main paired openings into the branchial cavity are :—

- (a) Posterior inhalent pair.
- (b) Anterior inhalent pair at the bases of the chelae.
- (c) Anterior exhalent pair near the mouth.

Pearson (99) has shown that in *Cancer* the posterior inhalent aperture plays only a small part in the respiratory current since most of the water enters by the anterior aperture. He suggests that the internal branchial ridge aids the water to reach the posterior gills before being drawn forward by the action of the scaphognathite. Zimmerman (136) has drawn attention to a small ridge near the base of the epimera in *Galathea*. This small prominence, although occupying a somewhat similar position to that in *Cancer*, does not seem significant to the present author, although its more prominent development in *Porcellana* may have some significance. Nicol (90) does not mention or illustrate an anterior inhalent water current for *Porcellana*, nor does Zimmerman make any observations on the relative strengths of the currents in the two inhalent apertures. If the posterior aperture carries the main intake current then the object of the ridge, as present in *Cancer*, is not significant.

In *Porcellana*, Zimmerman also noticed that the respiratory current was usually maintained by one side only, while the other side rested. Nicol confirmed and extended this work. In *Galathea squamifera* the respiratory current is usually maintained by both scaphognathites. Bohn (14) showed for *Carcinus* that a reversal of the respiratory current took place at intervals and suggested that this might rest the scaphognathite muscles and/or free the gill filaments from adhering particles. The number of reversals for a given time could be increased by the toxic influence of red seaweed juice. Zimmerman found in *Galathea* this reversal also took place, but that it was irregular and weak.

Zimmerman also emphasised the necessity of preventing mud, stirred by wave action, from entering the gill chamber. In *Porcellana* this was well effected by a thick curtain of bipinnate setae over the inhalent apertures. In *Galathea* these setae are simple and not so efficient. This deficiency is counterbalanced by the presence of epipodites whose brushing action cleanses the gill filaments. In *Porcellana* epipodites are absent. The correlation of these characters when applied to other members of the family shows frequent anomalies. In *G. nexa* and *Munida subrugosa*, both deeper water forms, the presence of epipodites is

also combined with an increase in the complexity of the filtering setae. Unknown factors may, however, account for this difference. In *P. longicornis*, where the epipodites are absent, the filtering setae are simple and of the *G. squamifera* type. This Zimmerman accounts for by the exceptionally clean-water habitat of *P. longicornis*. Nicol points out that *P. longicornis* and *P. platycheles* may both be found together in not too clean water at Plymouth, although the latter can be, and frequently is, found in muddier conditions. Zimmerman also states that species without epipodites thrust their chelate fifth pereopods into the branchial chamber to remove sediment, an action therefore which he implies is apparently not carried out by *Galathea squamifera*.

Nicol, however, reports that *G. squamifera* does perform this act and the present author can confirm this, having noted it on many occasions.

Branchiae (Text-Fig. 9, Plate XVI, Figs. 100-103)

In the decapods three main types of gills are recognisable (Calman 28) :—

- (a) Trichobranchiate.
- (b) Phyllobranchiate.
- (c) Dendrobranchiate.

Among the Anomura, the phyllobranchiate type is most predominant; Milne-Edwards (84), however, states that among the Galatheidae *Aeglea* is an exception. Calman (28) also points out that several genera of the Paguridae are trichobranchiate and the gills of some Thalassinidea are intermediate in character.

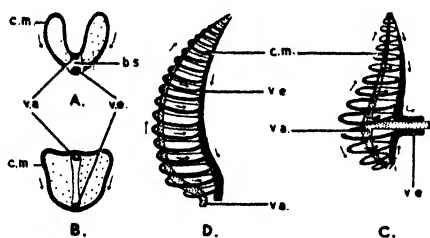
Within the Galatheidae the chief difference in the gill formula is in the reduction of the epipodites to one on the third maxilliped in *G. strigosa* and their complete absence in the Porcellanidae.

The table on page 91 shows the branchial formulae for *G. squamifera*.

In *Galathea squamifera* each branchia is of the phyllobranchiate type (Text-Fig. 9, A). The afferent and efferent veins are close together and joined by the connective tissue of the Branchial Septum (Text-Fig. 9, A, b.s.). To this septum a lamella is attached on each side, but because of the diminution of the base of

| | | | | | | | | |
|---------------------|---------|---|---|---|----|----|----|----|
| Somites | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| Thoracic Appendages | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Podobranchiae ... | ABSENT. | | | | | | | |
| Arthobranchiae ... | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 0 |
| Pleurobranchiae ... | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| Epipodites | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |

insertion, the lamellae compensate by protruding forward in the form of a broad " V " (Text-Fig. 9, A). The reduction in length of the branchial septum appears to be a progressive anomuran characteristic. It is greater in the Galatheidæ than in the Paguridæ, while in the Porcellanidæ the veins are almost contiguous. In the Brachyura (Text-Fig. 9, B.) the veins are separated by a wide septum so that the gill filaments form roughly a quadrilateral.



TEXT-FIG. 9

- A. A single phyllobranchiate gill lamella of *G. squamifera*.
 B. A single phyllobranchiate gill lamella of a brachyuran.
 C. The position of attachment and passage of blood through a phyllobranchiate gill of *G. squamifera*.
 D. The position of attachment and passage of blood through a brachyuran phyllobranchiate gill.

(Figures C and D modified from Drach (36).

b.s., branchial septum; *c.m.*, marginal canal; *v.a.*, afferent branchial vein; *v.e.*, efferent branchial vein.

Drach (36) has shown that the branchiae in the *Anomura* (Text-Fig. 9, C), are attached laterally to the body wall, while in the *Brachyura* the position of attachment is ventral. In the *Anomura* therefore the efferent and afferent veins branch both dorsally and ventrally from their body attachment (Text-Fig. 9, C), taking blood to and away from the gill filaments. In the *Brachyura* there is no need for such branching (Text-Fig. 9, D). Drach also remarks that the *Natantia* have branchiae which from the morphological point of view more closely resemble the *Anomura*, and more precisely the *Porcellanidae*, than those of the *Brachyura*,

It has been mentioned previously that the blood passes from the afferent to the efferent veins through the branchial lamellae (*vide* page 86). This passage is mainly by way of the marginal canal (Text-Fig. 9, c.m.). A small amount of the blood does pass through the intercellular spaces of the lamellae. Allen (3) states that for *Palaemonetes varians* all the blood travels by way of the marginal canals as the intercellular spaces are too small to allow the passage of corpuscles.

Histology of the Branchiae (Figs. 100-103)

[*Method.*—Both Allen (3) and Smyth (117) found a difficulty in obtaining good fixation of the tissue. For *Palaemonetes* Allen found that Flemming (strong) preserved both cell outline and protoplasmic structure in an excellent state. Smyth found that of the usual fixatives only Champy and Mann were satisfactory. It should be noticed, however, that he removed the gills from the body only when using these two fixatives, in the remainder the whole animal was immersed. Possibly the non-removal of the gills may have hampered the entrance of the fluid. It has been found that both Helly's and Gilson's fixatives gave a reasonable result with the gills removed, but better results were given with Champy's fluid.

Whole mounts were stained in chlorazol black E and haemalum.]

BRANCHIAL CUTICLE

The whole branchia is covered by thin cuticle which stains deeply with Weigert's iron haematoxylin and chlorazol black E. With Mallory's connective tissue stain the cuticle is found to be

thickened by a chitinous layer at the borders of the lamellae and also in the vicinity of the afferent vein. Smyth noted hairlike processes covering the outside cuticle in *Carcinus maenas*, but those were not seen in *Galathea*. What appear to be a number of channels are clearly visible, radiating outwards from the nuclei and perforating the cuticle (Figs. 102, 103, c.ex.c.).

BRANCHIAL SEPTUM

The epithelium of the branchial septum is formed by loose connective tissue in which the scattered nephrocytes or excretory cells are situated. Another batch of nephrocytes is found in the marginal channel of the lamina (*vide* page 94).

No tegumental glands were found in the tissue of the branchial septum, although numbers of them were recorded in that position in *Palaemonetes* by Allen (3) and Cuénot (30) noticed them in some of the *Brachyura*.

Both afferent and efferent veins are lined by a thin epithelial layer which is perforated along its course to allow the passage of blood to the lamellae.

BRANCHIAL EPITHELIUM (Figs. 101, 103)

Beneath the cuticle of the lamellae are situated two layers of epithelial cells. These cells are drawn out in places to form Pillar Junction Cells (Figs. 101, 103, p.j.c.), with the nuclei of the cells situated at the base of the pillars. These pillars may be divided by a transverse septum, or they may pass from one side to the other. The former condition (Fig. 103) is similar to that in *Carcinus maenas* (Drach, Smyth), while the latter condition (Fig. 101) is observed in *Maia* (Bernecker 8). In *Galathea* no regular disposition of these two types of cells has been observed. In whole mounts the pillars are seen to pass in somewhat regular rows from one side of the lamella to the other, that is, at right angles to the afferent and efferent portions of the marginal canal. This same disposition is found in the *Natantia*. In the *Brachyura* the rows are roughly parallel and follow the curvature of the marginal canal. The pillar bases are elliptically flattened in the direction of the rows, which facilitates the blood flow in that general direction. According to Drach the pillars are multi-nucleate,

each pillar having from three to ten nuclei. In *Galathea* there is usually only one nucleus at the head and one at the base of the pillar, but this number may be increased to two nuclei in each position. Situated among the pillar epithelial cells Drach also observed ordinary epithelial cells which were disposed usually with a certain regularity. These cells are relatively rare in *Carcinus*, more numerous in *Cancer* and usually found in numbers in the epithelium of the marginal canals. In *Galathea* these cells have only been seen in the marginal canal (Fig. 101, e.c.).

The cytoplasm of both marginal and pillar cells is traversed by deeply staining bands which penetrate the cuticle. In surface view these bands are seen to radiate out from the nuclei of the pillar cells (Fig. 102). It is not known whether these bands are real tubes as suggested by Smyth or merely the "tonofibrillae" of Drach. Cell boundaries could not be ascertained in *Galathea*, although they were observed in *Cancer* and *Carcinus* by both Drach and Smyth.

THE RETICULAR NETWORK AND NEPHROCYTES

A reticular network of cytoplasm was found by Drach (36) to span both the lamellae and the branchial septum in the Brachyura. This network in many ways resembles pillar cells from which it is probably derived. The network and nephrocytes are closely linked as they both appear on the reticular spans. In *Galathea* the Reticular Network (Fig. 101, ret.n.) and nephrocytes occupy two areas of unequal size in the marginal canal, but are absent in the branchial septum. The larger mass occupies a position about half-way along the efferent part of the marginal canal, while the smaller mass occupies the apex. In the Natantia one finds similar dispositions of the network in the lamina, but without the presence of nephrocytes which are only found in the branchial septum.

Nephrocytes (Fig. 101, n.) are spherical, vacuolated cells. A mature nephrocyte consists of a large vacuole filled with a yellow substance. The vacuole thrusts both the cytoplasm and the nucleus towards the periphery. Within the cytoplasm small white spheres are observed (Fig. 101, n.s.). In most Brachyura

and the Anomura the nephrocytes are simple cells, but in *Cancer* and *Upogebia* the nephrocytes are syncytial. Young nephrocytes are small ovoid elements containing a number of small colourless vacuoles, the main vacuole appearing at a later stage.

Bruntz (23, 24) and Drach (36) both think that these cells have an excretory function and the substance which accumulates in the central vacuole leaves the cell at the period of moult. This substance passes into the blood, but the factors controlling its diffusion and the destiny of the substance are unknown.

THE NERVOUS SYSTEM

For descriptive purposes the nervous system has been divided into two portions :—

1. Ventral Nerve Chain.
2. Stomatogastric Nerve.

Following the descriptions of these systems, an account is given of their blood supply.

1. The Ventral Nerve Chain (Plate XVII, Figs. 105, 106)

In *Galathea* this may most conveniently be described under the following three headings.

- (a) Supra-oesophageal Ganglion or Brain.
- (b) Thoracic Ganglionic Mass.
- (c) Abdominal Nerve Chain.

[*Method.*—The supra-oesophageal ganglionic mass and the stomatogastric nerve are best dissected from the dorsal or lateral side, while the thoracic ganglionic mass and the abdominal nerve chain are best viewed from the ventral side.]

(a) SUPRA-OESOPHAGEAL GANGLION

This ganglion (Figs. 105, 106, sp.g.) is situated anterior to the oesophagus and ventral to the cardiac portion of the fore-gut. It occupies a considerable area transversely and in shape is roughly rectangular. Within this mass are situated eight ganglionic aggregations or neuropiles. These neuropiles are directly associated with the nerves to the cephalic appendages.

Two thick connectives, one on each side of the oesophagus, pass posteriorly to connect with the anterior thoracic, or sub-oesophageal ganglionic mass (see below). These connectives give rise to the *Par-oesophageal Ganglia* (Figs. 105, 106, p.g.) which are situated on each side at the postero-lateral margin of the oesophagus. From these ganglia the stomato-gastric nerves arise (*vide* page 97) and behind the oesophagus the par-oesophageal ganglia are joined transversely by the *Post-oesophageal Commissure* (Figs. 105, 106, p.c.).

(b) *THE THORACIC GANGLIONIC MASS* (Fig. 105) is composed of two groups of ganglia. The anterior portion or *Sub-oesophageal Ganglionic Mass* (Figs. 105, 106, sb.g.) supplies the post-oral cephalic appendages and the anterior thoracic appendages, whilst the main thoracic ganglionic mass supplies all the pereopods and the first abdominal segment.

There are five pairs of ganglia in the sub-oesophageal ganglionic mass which, although closely packed, are quite distinct and each single ganglion gives rise to a pair of nerves. The most anterior ganglion gives off a single nerve to the metastoma and another to the mandibles, while the second ganglionic pair send a single nerve to each of the two maxillae. The posterior three sub-oesophageal ganglionic pairs innervate the three maxillepedes each of which receives two nerves.

In the *Main Thoracic Ganglionic Mass* there are six pairs of ganglia. The anterior five pairs are thoracic and supply the pereopods while the last pair, which is considerably reduced, is abdominal in origin and innervates the first abdominal segment.

Each pereopod receives two nerves. The ganglia of the first pereopods or chelae are very large and are joined to the remaining thoracic ganglia by short thick connectives. Between thoracic ganglia three and four a large foramen perforates the nerve mass, allowing the passage of the sternal artery (Fig. 95, s.a.).

The last pair of ganglia in the main thoracic mass is much reduced in size and, as stated above, innervate the first abdominal

segment. Two nerves arise from each of the first pair of abdominal ganglia, the first innervates the ventral thoracic muscles, the second nerve divides into two, the anterior branch innervates the first pleopod and the posterior branch the muscles of the second abdominal segment.

(c) THE ABDOMINAL NERVE CHAIN (Figs. 105, 106)

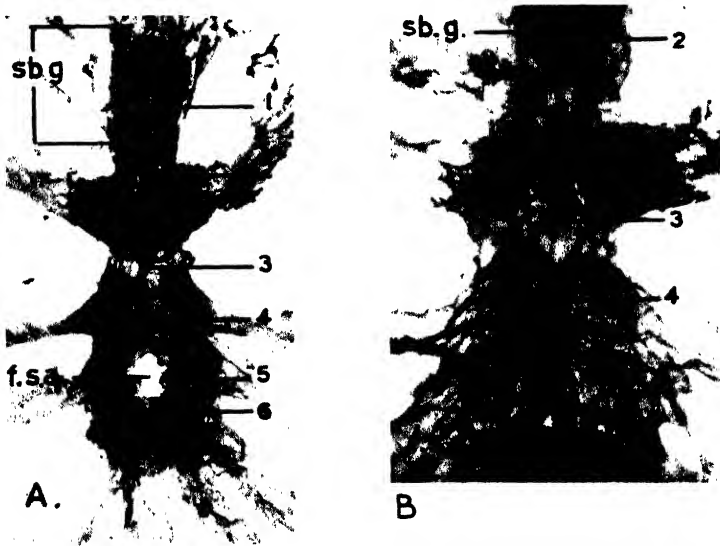
Five pairs of ganglia are situated within the abdomen. The first pair are situated at approximately the centre of the second abdominal segment and are joined to the thoracic mass by two long, closely applied connectives. The remaining four ganglia are joined by short connectives which are quite distinct. The posterior nerves from the penultimate ganglionic pair are reduced. The terminal ganglion gives off three pairs of nerves: the anterior pair innervating the pleural area of the sixth abdominal segment, the second pair the uropods and the posterior pair the telson. The situation of the terminal ganglionic pair is within the fifth abdominal segment, thus an attenuation of the abdominal nerve chain has begun in the Galatheidæ and is carried further in the Porcellanidæ (*vide* page 99).

2. **The Stomatogastric Nerve** (Figs. 105-107)

This nerve originates from the two par-oesophageal ganglia (Figs. 105, 106, p.g.). The nerves, after passing forward round the oesophagus, join in the middle line to form the *S t o m a t o - g a s t r i c N e r v e* (Figs. 105-107, s.n.). Two ganglia appear to be present at this junction, of which the ventral ganglion is smaller and gives rise to a short nerve to the labrum. From the dorsal ganglion the stomatogastric nerve, now single, passes dorso-anteriorly and at approximately the mid-point of the cardiac plate of the fore-gut, a swelling marks the position of the *S t o m a t o g a s t r i c G a n g l i o n* (Figs. 105-107, s.g.). Three nerves are given off from this ganglion. Two lateral branches innervate the anterior gastric muscles (Fig. 107, a.g.m.), whilst the median dorsal branch passes between these muscles and over the dorsal surface of the fore-gut. Just posterior to the urocardiac ossicle the nerve divides into two branches. These branches pass ventrally and innervate the intrinsic muscles of the fore-gut.

Blood Supply to the Nervous System

In *Eupagurus* Bouvier (17) noted arterioles penetrating the thoracic mass. These penetrations are effected between the connectives joining the sub-oesophageal ganglionic mass and the main thoracic ganglionic mass, between the ganglia of the first and second pereopods and between the ganglia of the second and third pereopods, thus making three penetrations into the thoracic mass anterior to the main penetration of the sternal artery.



TEXT-FIG. 10

Thoracic ganglionic mass of *G. squamifera*, photomicrographs showing :—

A. Two arterioles penetrating the sub-oesophageal ganglionic mass (*sb.g.*, 1, 2) and four penetrations (3-6) in the main thoracic mass. $\times 3$.

B. The profusion of the ganglionic blood supply. $\times 4\frac{1}{2}$.

f.s.a. Foramen for sternal artery.

In *Galathea*, with the exception of the sternal artery, no mention has been made of blood vessels penetrating the thoracic mass. Actually penetration takes place at six points (Text-Fig. 10). Two are in the sub-oesophageal ganglionic mass (Text-Fig. 10, A, *sb.g.* 1, 2), and four in the main thoracic mass (Text-Fig. 10, A,

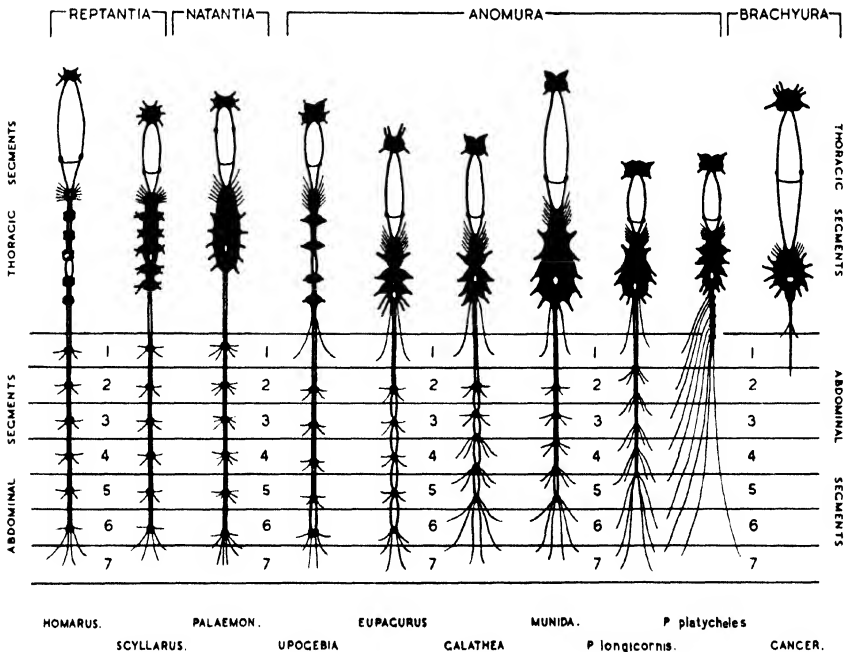
3-6). The most posterior arteriole (6) divides and sends branches between the fourth and fifth, and fifth and sixth ganglia. Thus, except in the sub-oesophageal ganglionic mass arterioles penetrate between each pair of ganglia.

Histology of the Nervous System

The histology of the nervous system in Crustacea is a rather too specialised study to come within the scope of this work. Reference should be made to papers by Allen (4), Bethe (9), Retzius (III), and Holmes (64).

Comparative Morphology of the Nervous System

Within the Anomura a complete series is to be found, beginning with the extended nerve chain of the Thalassinidae and ending with the contracted condition of the Porcellanidae (Text-Fig. II).



TEXT-FIG. II

Comparative nervous systems of Crustacea. These are represented diagrammatically and are not drawn to scale. The position of the abdominal ganglia within the abdominal segments is relatively correct.

Within the Thalassinidae, Bouvier (17) has described the nervous system both of *Axius* and of *Upogebia*, although the latter system is less fully described. In *Axius* he draws attention to the fact that the sub-oesophageal ganglionic mass has distinct ganglia and that the last ganglion is differentiated both from the others and also from the main thoracic mass. Everywhere else in the main thoracic mass there is complete separation between both ganglia and connectives. In the abdominal chain there are six pairs of ganglia.

Upogebia differs from *Axius* in that the first pair of abdominal ganglia are found towards the posterior extremity of the thorax being followed by five ganglia within the abdomen.

Within the Paguridae the nerve supply was noted by Bouvier to be closely akin to that of the Thalassinidae, but is more concentrated antero-posteriorly in the thorax, while in the abdomen the same five pairs of ganglia are distinct.

The thoracic mass, although without inter-connective spaces, shows the vestiges of those spaces by the penetration of the small arterioles from the ventral thoracic artery. This is also a characteristic of the Galatheidæ (*vide* page 98). In *Eupagurus* the last two pereopods are reduced and both are innervated from the last pair of thoracic ganglia which are small. Nerves to the first abdominal segment also arise from these ganglia.

Five pairs of ganglia are present within the abdomen, the first pair being situated in the second abdominal segment.

Within the Galatheidæ the general arrangement of the ventral nerve differs little from that of the Paguridae except that the last two pereopods are innervated from separate ganglia and the first abdominal segment has a distinct ganglionic pair in the thoracic mass.

In *Munida*, although there is a change in shape of the main thoracic mass, the positions of the ganglia are the same as for *Galathea* both in the thorax and in the abdomen. The ventral nerve chain of *Porcellana longicornis* closely resembles that of *Munida* in its arrangement, the only major difference being that in *P. longicornis* the abdominal chain has become somewhat attenuated and the last abdominal ganglion lies between the

fourth and fifth abdominal segment. In *P. platycheles* the abdominal chain has become much shorter, but the five pairs of ganglia are still distinct.

Thus within the Anomura one finds a range of conditions from the extended chain of *Axius* to the compacted ganglionic mass of *P. platycheles*. The most striking feature of these systems is the innervation of the first abdominal segment from within the thorax, and five pairs of ganglia within the abdomen. This appears a constant anomuran characteristic except in the Thalassinidae, for in *Upogebia* the first abdominal ganglion although within the thorax is not fused with the main thoracic mass, while *Axius* has six pairs of abdominal ganglia all situated within the abdomen.

Within the Reptantia, *Homarus* has an extended thoracic chain whereas *Scyllarus* has a condensed thoracic mass although the constituent paired ganglia are still distinct (Text-Fig. 11). Within the abdomen of each there are six pairs of ganglia.

Within the Natantia, *Palaemon*, the thoracic mass is compacted, but the abdominal chain consists of six pairs of ganglia as in *Scyllarus* and *Homarus*.

Within the Brachyura, *Cancer*, the thoracic mass is still further compacted and the abdominal chain is absent (Text-Fig. 11). In the more primitive Dromiacea (Calman 28) the concentration is somewhat less complete. The outlines of five pairs of ganglia can be distinguished in the thoracic mass while posteriorly there is a shortened chain of five ganglia which do not extend beyond the thorax. In this *Dromia* appears strongly to resemble *Porcellana platycheles*.

SENSE ORGANS

The Eye (Plate XVIII)

[Method.—The optic peduncle was removed and fixed in Helly or Bouin Duboscq-Brasil. This latter was found to give better results which was probably due to deeper penetration. The whole eye peduncle was embedded in paraffin wax and also in ester wax. This latter method, developed by Steedman (119), was a great improvement on the paraffin wax and the methylene blue erythrosin staining

detailed for this method was very satisfactory. The paraffin sections were stained with Weigert's iron haematoxylin and erythrosin.]

In *Galathea*, as in most decapods without reduced eye-stalks, a part of the supra-oesophageal ganglion, the medulla terminalis (Fig. 108, m.t.), together with the three primary optic centres, have migrated into the eye-stalk and are connected with the main supra-oesophageal ganglion by the pedunculus lobi optici, or optic nerve (Fig. 108, p.l.c.). The ommateum is connected by nerve elements to the terminal optic centre, the lamina ganglionaris (Fig. 108, l.g.). From the outside the ommateum forms a black hemi-spherical end to the eye-stalk, whose margin is indented on the dorsal and ventral sides by two small prolongations of the calcified eye-stalk integument.

For descriptive purposes the eye will be divided into two parts. The terms applied to the cells forming the ommateum are those used by Parker (95) and for the optic centres they are taken from Hanström (56).

(i) The Ommateum.

(ii) The Optic Centres, the Sinus Gland and the X-organ.

THE OMMATEUM (Plate XVIII, Figs. 108, 109, 110)

Each ommatidium consists of a cluster of cells grouped round a central axis which is composed of the cones and the rhabdome. The cells are, from the outside inwards: the corneagen cells which form the facets; the cone cells giving rise to the cones; the distal and proximal reticular cells which sheath the rhabdome; the basal pigment cells and the accessory pigment cells.

The Cuticular Facets (Figs. 109, cu.f., 110, A.) are square in *Galathea* and made up of an outer cuticular layer and an underlying pigmented layer. These square facets were first noticed by Will (126) in *G. strigosa*, although according to Patten (98) the facets are hexagonal in an unnamed species of *Galathea*. The present author finds that all the British species of *Galathea* have square facets and this is confirmed by Bernard (7) for *G. squamifera*, while Williams (128) states that square facets are present in *Porcellana platycheles* in both the larva and in the adult. Hexagonal facets are, however, present in the Anomura in

Eupagurus, Jackson (67) and in *Gebia* and *Callianassa*, Will (126). Parker (95), who has discussed at some length the significance of the tetragonal and hexagonal arrangement, thinks that the hexagonal plan is phylogenetically the older.

The Corneagen Cells (Fig. 109, cn.c.) are two flat cells which lie immediately below each cuticular facet to which they give rise. The four Cone Cells (Figs. 109, co.c., 110, B.), each of which has a nucleus on the outer edge just proximal to the triangular apex of the cells, separate the two corneagen cells. The cones lie immediately below the cone cells and taper gradually to their rounded proximal ends where they are cupped by the somewhat swollen distal portion of the rhabdome. The cones are screened by the Distal Retinular Cells (Figs. 109, d.r.c., 110, B.), of which there are probably two. These cells are heavily pigmented and each appears to screen two sides of the quadripartite cone (Fig. 110, B.). At the level of the junction of the cones with the rhabdome, the distal retinular cells merge with the proximal retinular cells. The Proximal Retinular Cells (Figs. 109, p.r.c., 110, C.) ensheath the whole length of the rhabdome and the swollen distal portions contain six nuclei. The seventh nucleus is situated just above the proximal swelling of the rhabdome, between it and the heavily pigmented cell (Fig. 109, p.p.c.). In transverse section (Fig. 110, C., no nuclei shown) the distal nuclei are seen to be arranged on two opposite sides of the rhabdome, but without depigmentation it is not possible to work out the relationship of these cells. If however a transverse section is taken through the base of the rhabdome (Fig. 110, E.) seven cells are clearly seen to be present which is the typical number of proximal retinular cells for decapods. Dobkiewicz (34) in his work on the eyes of deep sea Galatheidæ gives an illustration of the eye of *G. squamifera* in which a similar arrangement to that shown in Fig. 109 is portrayed. The Rhabdome (Fig. 109, rh.) is swollen at the distal end which cups the cones, but fusion of the rhabdome with the cones has not been observed. Proximally it suddenly decreases to a narrow shaft, but swells again before tapering away just distal to the basement membrane. In longitudinal section the proximal swelling shows bands of

pigment at both ends. This suggests a formation similar to that described by Parker (95), but it is not so pronounced as that illustrated by Jackson (67) for *Eupagurus*. Additional Proximal Pigment Cells (Fig. 109, p.p.c., 110, D.) also appear to be present. There are three of these cells clearly shown in transverse section (Fig. 110, D.), the largest cell occupying the space between four neighbouring rhabdomes. This is very evident in longitudinal section (Fig. 109, p.p.c.) by its heavy pigmentation, and may send a tongue of pigment distally as far as the anterior swelling of the rhabdome. Below the posterior swelling another nucleus is seen closely applied to the ommatidium which probably represents the Accessory Pigment Cell (Fig. 109, a.p.c.) of Parker (95). These cells fill the space between the proximal ends of the ommatidia and extend from the basement membrane to the middle of the rhabdome. The pigment has the quality of reflecting light and is not easily seen in sections.

THE OPTIC CENTRES (Plate XVIII, Fig. 108)

The medulla terminalis (Fig. 108, m.t.) is connected proximally with the supra-oesophageal ganglion by the pedunculus lobi optici (Fig. 108, p.l.c.) and distally to the three optic centres by thick connectives.

The three optic centres are, proximally-distally :—

- (a) Medulla interna (Fig. 108, m.i.).
- (b) Medulla externa (Fig. 108, m.e.).
- (c) Lamina ganglionaris (Fig. 108, l.g.).

Both the medullae are compact masses of nervous tissue banana-shaped in vertical longitudinal section. Their actual relative positions may vary within the same species, but usually they make an angle of about 30° with each other; diverging towards the dorsal side. The lamina ganglionaris, which is situated nearest the ommatidia receives nerve fibres from the proximal reticular cells through the basement membrane.

The Sinus Gland (Plate XVIII, Figs. 108, 111)

All the optic centres are surrounded to some extent by heavily staining nerve cells and on the dorsal side there is a dorso-lateral inner blood sinus (Figs. 108, 111, i.s.), the whole being sheathed

by neurilemma. On the outside of the neurilemma there is a larger outer blood sinus (Figs. 108, 111, o.s.). The Sinus Gland (Figs. 108, 111, s.gl.) is a thick walled cup-shaped structure, the inside of which is lined with a structureless membrane. The body of the gland is formed of a spongy tissue in which scattered nuclei are situated. It appears to be similar in shape, texture and position to the sinus gland described for *Munida* and *Eupagurus* by Sjögren (116) and also resembles that for the prawn *Acantheephyra purpurea* described by Hanström (57, 58, 59). The inner and outer blood sinuses communicate directly through the gland and not through its offshoots of which there are two or three (Fig. 111, s.gl.1). The walls of the gland are connected with the medulla terminalis by a thick nerve, which in its course passes through a mass of glandular cells on the dorsal side of the medulla (Fig. 108).

Hanström also states that in several Anomura with reduced eyes the sinus gland is no longer in the eye-stalk but within the head. In these (*Hippa*, *Emerita*, *Gebia*, *Calocaris* and *Callianassa*) the structure of the gland has probably been secondarily simplified. It is not flat as in the Mysidacea but sharply separated from the supra-oesophageal ganglion, having the structureless membrane on the outer side, and no free space on the inner side. On account of this special structure, Hanström (56) has called this type of gland "everse" whereas the other type, to which *Galathea* appears to belong, is called "inverse."

According to Perkins (104) and Hanström (59) extracts from the eye-stalk influence the contraction of the chromatophores, and Hanström considers that the incretory organ in the eye-stalk responsible for secreting this substance into the blood is the sinus gland. Thus this gland produces the hormone (or hormones) which control the contraction of the red and yellow chromatophores in decapods except in the Brachyura, in which it controls the expansion of the red and black chromatophores.

The X-organ (Plate XVIII, Figs. 108, 112)

The X-organ (Figs. 108, 112, x.) is found in *Galathea* situated on the ventral side close to the medulla terminalis to

which it is connected by a thick nerve. As in the Natantia, the organ is shaped like a cluster of grapes; each separate cluster, containing several X-cells, is surrounded by neurilemma.

According to Hanström (56) the X-organ appears originally to have been a sensory or nervous structure. It later became vestigial and transformed into an endocrine organ, but its function is not yet fully understood.

In several Anomura with more or less reduced eyes (*Gebia affinis*, *Upogebia deltaura*, *Hippa talpoida*, *Emerita analoga*) the position of the X-organ is again in the anterior part of the cephalothorax in close proximity to the supra-oesophageal ganglion.

The Statocyst (Plate XIX, Figs. 113, 114, 115)

The statocyst of *Galathea*, as in other Reptantia, is situated within the basal joint of the antennule. It is suspended from the dorsal wall of this joint and is in communication with the exterior through a narrow median slit. This slit is widest at the proximal end and is there covered by a tongue-like scale projecting forward from its posterior margin (Plate IV, Fig. 18, sc.). The aperture of the slit decreases anteriorly and this lid, or tectum, is edged with closely packed plumose setae, which cover the slit and exclude extraneous matter. These setae lengthen posteriorly and pass under the tongue-like scale of the posterior portion, and it would be difficult for any sand grains to be inserted under this scale after moulting and hardening had taken place.

The sac of the statocyst extends almost throughout the length of the basal joint of the antennule and is more than twice as long as it is broad. In a full-grown specimen the length of the statocyst is 3 mm. and its greatest width 1.5 mm. The opening extends along the anterior two-thirds of the statocyst (Fig. 114), the proximal third of the latter is prolonged backwards into a tube-like extension which is separated from the broad distal portion by a specially deep constriction in the region of the proximal commencement of the slit (Fig. 114). In this extension are situated the setae to which the sand grain statoliths are attached (Figs. 114-115, stat.s.).

Kinzig (69) accurately described the internal structure of the

statocyst of some decapods, including that of *Galathea strigosa*. *G. squamifera* (Figs. 113, 114) differs in no respect from its larger relative. The statocyst is a complex irregular sac which is not easily described so that the figures will have largely to replace a verbal description. The most striking feature of the organ is the deep keel-like invagination which projects into the lumen horizontally from the outer ventro-lateral edge (Figs. 113, 114, k 1 broken line). The keel is narrow, the two walls of the keel meet along the median edge and are separated elsewhere by connective tissue. The keel projects almost half way across the lumen of the statocyst and in the constricted anterior portion almost divides the lumen into a dorsal and a ventral chamber. In some species of *Galatheidae* including *G. squamifera* and *Munida bamffica* there is a second smaller keel just posterior to the one already described (Figs. 113-114, k 2).

The statocyst wall is calcified in some areas but for the most part it is composed of clear non-calcified chitin. The cellular derivation of the outer layers can be clearly seen in transverse section and in whole mounts. The average thickness of the cyst wall is 12μ but this may be doubled where calcification has occurred. The ventral wall of the statocyst is perforated by numerous fine canals directed obliquely forward and these appear to be the ducts for tegumental glands. The method of attachment of sand grains to the setae of the statocyst by the secretion of the tegumental glands suggested by Prentiss (1907) has been described in *Homarus* by Lang and Yonge (1972).

STATOCYST SETAE

The statocyst setae are of two types :

- (i) Plumose.
- (ii) Simple.

The plumose setae (Fig. 115, a.) are only found in association with the statoliths in the proximal tubular portion of the statocyst, where between eight and ten setae appear to be situated on the ventral wall (Figs. 114, 115a, stat.s.). The sand grains are so firmly attached to these setae that separation is extremely difficult.

The simple setae (Fig. 115, b.) are found in two regions. A long curved row of about thirty setae lie in the median ventral groove (Fig. 113, s.s. 1), these are very delicate and the present author has not been able to see the pinnate structure described by Kinzig. The other set of simple setae are larger and taper from the bulb-like base to an extremely fine tip (Fig. 115, b.). Kinzig termed these the median statocyst setae. These are about thirty in number and they are found irregularly scattered over the latero-median wall (Fig. 113, s.s. 2).

All the statocyst setae are delicate and not easy to locate, they vary from 130μ to 300μ in length and both types have deeply sunk bulbous bases giving free movement.

Comparison of Statocysts

From the work of Henson (61), Prentiss (107), and Kinzig (69) it appears that the statocysts of the Reptantia fall into two main groups :

- (i) Statocyst open and containing statoliths in both the larva and adult.
- (ii) Statocyst closed and without extraneous statoliths in the adult.

The Palinura, Astacura, Anomura and Dromiidae have statocysts of the first type ; all the Brachyura with the exception just noted possess statocysts of the second type.

It is difficult to distinguish between open and closed statocysts in such species as *Porcellana*, *Coenobita* and *Dromia* owing to the narrowness of the opening. In *Porcellana* and *Coenobita* there appear to be no statoliths and according to Kinzig the statoliths of *Dromia* are formed of calcium carbonate. The external aperture of the statocyst of this genus is also situated on the lateral instead of the dorsal face of the antennule as in other genera. The above three genera therefore do not strictly fit into group (i), but have been placed there because of the open statocyst.

The statocysts of the Anomura are very variable both in shape and in the number and position of the setae. Because of this variability it has been found impossible to use the statocyst for

illustrating relationship within the Anomura, although Shen (114) found it of some value when dealing with the Natantia. Even within the Galatheidea there is considerable variation, in the family Galatheidæ *Munida* and *Galathea* are closely akin, but the characteristic keel-like invagination seen in these two genera is absent, or very rudimentary, in *Porcellana*. In this latter genus the present author has not been able to find statoliths and owing to the smallness of the external aperture this is not surprising, but the general form of the statocyst resembles that of *Galathea*. Even more marked differences have been noted by Kinzig within the Paguridae. The similarity between *Lithodes maia* and *Eupagurus* noted by this author are understandable when it is remembered that they are both members of the same tribe, since *Lithodes maia* is not, as he supposes, a member of the Brachyura.

Olfactory Organs (Plate XIX, Figs. 116, 117)

The essential constituents of the olfactory organ are the olfactory setae, the terminal nerve, the olfactory spindle and the olfactory nerve. The whole of this apparatus is situated within the third joint of the antennule, at the end of which two flagella are situated. The longer outer flagellum bears on its inner side the Olfactory Setae (Fig. 116, olf.s.). These hollow setae are closed distally so that no direct chemical stimulation of an exposed nerve ending is possible.

Also it cannot be proved that the terminal nerve strand (Fig. 117, term.st.) passing from the olfactory spindle to the seta base penetrates to the end of each seta. One must suppose therefore that olfactory stimulation takes place through the cuticle of the seta. The Olfactory Spindle (Figs. 116, 117, olf. sp.) is a large crowded mass of sensory cells termed the Lobus Osphradicus by Doflein. (35). From the spindle a number of nerve fibres come together to form the Olfactory Nerve (Figs. 116, 117, olf.n.) which passes down the antennule to the supra-oesophageal ganglion. A branch from the olfactory nerve is given off to the inner flagellum at the proximal end of the third antennal joint.

Doflein differentiated three types of olfactory organs :

- (i) The olfactory spindle is situated within the outer flagellum.
- (ii) The olfactory spindle is not wholly contained within the outer flagellum, but also extends into the distal portion of the third joint of the antennule.
- (iii) The olfactory spindle lies wholly within the third joint of the antennule.

Marcus (82) who studied in detail the olfactory organs of the Galatheidea states that there is complete absence of the first type within the tribe, while the second and third types occur in about equal proportions. *Galathea squamifera* (Figs. 116, 117) can clearly be included in the second category. Marcus further subdivides types (ii) and (iii) according to their typical representatives:

- (a) *Uroptychus* type.
- (b) *Munida* type.
- (c) *Petrolisthes* type.

This subdivision is not considered necessary for the present work and for further details reference may be made to the paper by Marcus (82).

Doflein also found in the Brachyura on the distal end of the antennal joint a prickly basket of setae (Stachelkorb), which Marcus, also Milne-Edwards and Bouvier (84), noticed in some Galatheidae. The latter remarked that these hollow bristles should be supplied by a nerve and Marcus has observed this nerve branching off from the olfactory nerve at the base of the third antennal joint. The function of these setae is doubtful, they are probably tactile and may also give some protection to the olfactory setae from accumulation of sediment.

REPRODUCTIVE ORGANS

The sexes of fully-grown specimens may be differentiated at a glance if the adults are obtained in the spring or summer. In

such specimens the chela of the male shows the male characteristics (*vide* page 21), whilst the abdomen is very much narrower than in the female. These characters are largely lost in the autumn, but the sexes may always be differentiated by the pleopods (*vide* page 23).

Male Reproductive System (Plate XX, Figs. 119-121)

The standard work on the male reproductive organs of Decapoda is still that of Grobben (50) whose observations on *Galathea* are very accurate. Mouchet (87) has also described in detail the male system in the Paguridea and, to a lesser extent, that of the Galatheidea and Brachyura.

The whole male genital system consists of two testicular masses spread over the dorsal surface of the digestive diverticula. Each leads posteriorly into a coiled vas deferens which ultimately leads to the male genital aperture situated on the face of the coxa of the fifth pereopod on each side (Fig. 119, v.d.).

Each Testicular Mass (Fig. 119, te.) is essentially a long, extremely coiled tube giving the appearance of a solid organ. The anterior portions overlie the anterior part of the cardiac foregut, while posteriorly the two sides make contact beneath the posterior gastric muscles. Without cutting sections it is difficult to ascertain whether the two sides actually fuse. Mouchet (87) states that cross connection is made but that this is very fine and does not produce spermatozoa.

The Vas Deferens (Fig. 119, v.d.) of each side is given off at the level of the heart, the left occupies a more dorsal position than the right and extends further posteriorly owing to the sternal artery (s.a.), preventing further extension on the right side. Passing above the ventral muscles of each side the two vasa deferentia descend sharply to their external openings.

Each vas deferens begins with two thin straight portions between which is a closely packed spiral. Further on two spirals coiled in reverse are found, each having about eleven coils. Shortly after the last spiral the diameter of the duct suddenly increases and continues as an irregular convoluted tube to its orifice.

Sections through the uppermost part of the vas deferens show the lumen to be packed with a mass of spermatozoa as if a continuous flow were taking place, but at the change in direction of the third spiral this mass breaks into lengths separated by intervals without spermatozoa. Each successive spermatozoan mass is attached to a basal ribbon; it is sausage-shaped and covered by a delicate membrane. Throughout the third spiral the basal length of the spermatozoan masses as well as the distance between them progressively shortens, while their height increases. As the height increases the capsular coat thickens so that eventually a row of tall closely packed spermatophores is formed and fixed in single file to the basal ribbon (Fig. 120, c.).

This basal ribbon acts as a conveyor belt and at the point where the diameter of the vas deferens increases the ribbon conveying the spermatophores oscillates from side to side in a sinuous fashion. Each oscillation carries some eight or nine spermatophores and soon the distance between successive oscillations sharply decreases until the cavity of the vas deferens contains a broad band of capsules eight or nine abreast (Fig. 120, d.). This broad band continues throughout the remaining length of the duct, but on extrusion the ribbon is again unwound so that the spermatophores are extruded in single file. They remain attached to the ribbon which is placed by the male on the pleopods of the female during pairing.

The reversely coiled spirals found in *Galathea* are analogous to those found in certain Paguridea, but according to Mouchet (87) the vasa deferentia in the Paguridea are rather markedly subdivided into regions. Grobben (50) divided the vasa deferentia of decapods into three distinct regions; an efferent portion from the testis formed of flat cells, which gave way to a long celled granular portion and this in turn led into the muscular portion of the ductus ejaculatorius. In the present instance these areas are not clearly delimited and it does not therefore seem advisable to try and distinguish these areas in the vas deferens of *Galathea*.

Each spermatophore is bullet shaped, having a width of 15μ and a height of 70μ (Fig. 121). According to Block (12) the spermatophores dehisce at the moment the eggs leave the oviduct.

Histology of the Vas Deferens

Grobben (50) has given an account of the general histology of the vas deferens ; Mouchet (87) dealt at length with the histology of the vas deferens of the Paguridea and to a lesser extent with that of the Galatheidea and the Brachyura and showed that the vas deferens was composed of two distinct layers.

(a) External muscular layer.

(b) Internal glandular layer of varying thickness but always thicker than the external muscular layer.

(a) The External Muscular Layer (Fig. 120, A.B., mus. l.) in *Galathea* is composed of flattened cells and muscle fibres, the latter forming a network crossing each other at an angle of about 60° ; no longitudinal muscles were observed. Mouchet considered that the breaking of the continuous sperm flow in the last spire is brought about by the contraction of these muscles. More posteriorly the muscular layer becomes thinner (Fig. 120, D.) but thickens again as the terminal portion of the vas deferens is reached.

(b) The Glandular Layer (Fig. 120, A-D, grn. l.) is responsible for the formation of the various parts of the spermatophore and the ribbon to which they are attached. Until the end of the first spire all the cells are identical and nearly as long as they are broad (Fig. 120, A.). In the second and third spire (Fig. 120, B.C.) cell differentiation into three areas takes place. Dorsally and ventrally the cells begin to shorten (Fig. 120, B.) and this continues until they are only a fraction of their original height (Fig. 120, C., d.c., vent.c.), but the nuclei throughout are situated in their basal third. Between these two areas, the cells on each side increase in height (Fig. 120, C. lat.c.), while their nuclei are situated in the upper third. These changes in cell proportion cause the lumen to become elliptical and this is responsible for the moulding of the spermatophores. The cytoplasm of the lateral cells is not so dense and according to Mouchet they secrete the substance responsible for forming the spermatophore sheath and the ribbon to which the spermatophores are attached. This secretion, which accumulates in the ventral gutter is, in the anterior part, stained by basic dyes and forms a

continuous sheath to the spermatozoan masses. More posteriorly the secretion that forms the pedicels of the spermatophores and the ribbon to which they are attached stains with acidic dyes (Fig. 120, C.D., black).

After the dilation of the vas deferens (Fig. 120, D.) the arrangement of the cells and spermatophores completely changes. The tall lateral cells have quite disappeared while the short dorsal cells have elongated to form a ridge projecting into the lumen, this secretes a basically staining substance similar to that secreted by the tall lateral cells of the anterior part. The nuclei of this area are still basally situated and the walls separating the cells are difficult to distinguish. Below the spermatophore ribbon the cells are very flat, deeply staining and no divisions could be seen separating the individual cells.

Fasten (43) shows ciliated cells as being present in the vas deferens of some American Decapoda including *Pagurus setosus*. No definite cilia have been seen by the present author bordering any of the cells in the vas deferens of *Galathea squamifera*. It is possible that they are present in the wider portion of the vas deferens bordering the dorsal ridge-like mass of cells (Fig. 120, D.).

The Spermatozoa (Plate XX, Fig. 122)

The spermatozoa of *Galathea* are of the usual crustacean type, characterised by the absence of motile flagella at all stages in development and by the presence of a capsule.

The following description of the spermatozoa of *Galathea squamifera* is taken from the work of Block (12).

The capsule is pyriform 7μ high and 1.5μ broad at its widest part (Fig. 122, cap.) It contains a central canal and a long slender trigger but no visible operculum, and is joined to the ovoid nucleus (Fig. 122, nu.) by a collar from which three long stiff spines arise. The collar contains a prominent centrosome.

Spermatogenesis hardly comes within the scope of the present work; for an account of this process in *Galathea* reference should be made to the detailed work of Koltzoff (70).

Block found that the spermatozoa of Crustacea have a considerable taxonomic value and further mention of his observations

will be found in the comparative morphology of the reproductive system (*vide* page 116).

The Female Reproductive System (Plate XX, Fig. 118)

The female system (Fig. 118, ov., ov.d.) occupies a position comparable with that of the male and is situated entirely within the thorax. The ovaries are covered by a follicular epithelium and anteriorly occupy a position dorsal to the digestive diverticula on each side of the cardiac fore-gut. The two sides are joined beneath the posterior gastric muscles and continue ventral to the heart on each side of the intestine to the limit of the thorax. Two short oviducts pass laterally over the ventral muscles and lead to the exterior through openings on the faces of the coxae of the third pereopods (Fig. 118, ov.).

In October the ovaries are immature, white and compact, but early in the new year they are ripe, bright orange and occupy all the available space within the thorax. If at this period the ovaries are removed and fixed, the immature eggs of the second brood can be seen scattered among the mature eggs, but do not appear to arise from any conspicuous centre.

Only a rough estimate can be given of the time required for the embryo to develop. In some years in the South of England egg laying begins in December, but usually this does not take place until January-February. By March, nearly all the females are in "berry" and internally the ova of the second brood are reaching maturity. This would give a developmental period of from three to four months.

Histology of the Female Reproductive System

The histology of the oviduct has been omitted as it is unlikely to show anything further than that already described for *Homarus* by Yonge (135).

Oogenesis does not come within the scope of this work and reference should be made to the papers by Harvey (60) and Subramaniam (121).

DEVELOPMENT

The embryonic development has not been investigated for *Galathea* but probably differs little from that of other Decapoda.

Bumpus (26) and Herrick (62) have studied the embryology of *Homarus*, while Terao (122) has written fairly fully on the development of the spiny lobster *Palinurus japonicus*.

The post larval stages of the Galatheidea have been studied very ably by Lebour (75, 76), and Williams (128) has made a preliminary anatomical survey of the pre-zoea stage of *Porcellana platycheles*.

Pairing

All the references so far seen for the Natantia, Astacura and Brachyura suggest that moulting in the female is an essential preliminary to pairing and that the latter process is almost immediately followed by egg laying.

In the Anomura, Block (12) states that in *Diogenes pugilator* the male grips the mollusc shell housing the female until moulting has occurred. This is immediately followed by pairing when the spermatophores are transferred to the female's abdomen.

In *Galathea* the spermatophores are placed on the pleopods of the female but no direct observation of pairing has been made. In order to acquire "breeding dress" for the first brood the female must moult prior to pairing and egg laying. It is not known, however, whether pairing takes place immediately after moulting, as would be expected bearing in mind the behaviour of other decapods. Observations by the present author suggest that this is not necessarily the case.

Comparative Morphology of the Reproductive System

The female reproductive system appears to show little of comparative importance and so the remarks in this comparison will be confined to the male system.

In the Palinura and Astacura the male reproductive organs lie entirely within the thoracic cavity. In the Astacura the vas deferens is short, but in the Palinura it is much longer. In both groups the spermatophores are non-pedunculate and in some genera are inserted into special external pouches during pairing.

In the British genera of Galatheidea seen by the author

(*Galathea*, *Munida*, *Porcellana*) the reproductive system lies entirely within the thorax. This does not appear to be universal as Fasten (43) describes the male reproductive organs of the American species of *Petrolisthes eriomerus* as being situated within the abdomen. The vas deferens in all genera is long and the anterior portion possesses two coils wound in opposite directions. The spermatophores are pedunculate, produced in large numbers and placed on the abdomen of the female.

In the Thalassinidea (*Gebia*) the male reproductive system does not appear comparable with that of other Anomura, but only an inadequate account, given by Ishikawa (66), has been seen.

In *Dromia* the male reproductive system is situated within the thorax and in external appearance the vas deferens resembles that of *Galathea* although the two reversed coils are not present. In the anterior portion, according to Mouchet (87), the sperm flow is ensheathed by a highly refractive substance and in the posterior portion the tube is filled by a mass of globules. These must be extruded prior to the spermatophore and it is probable that this forms the temporary receptaculum within the female oviduct at the time of pairing.

In the Brachyura the vas deferens is provided with caecal diverticula which in some cases are very numerous. In the female the oviduct has a spermatheca for reception of the non-pedunculate spermatophores.

Block (12) found that the spermatozoa of Crustacea have a considerable taxonomic value. In the Natantia the spermatozoa lack a capsule and have a single spine with a voluminous undifferentiated protoplasmic head. The nucleus is sub-spherical and opposite the base of the spine.

In the Reptantia the spermatozoa have a capsule and more than one spine. They can be divided into two groups :

- (a) Capsule and nucleus distinct and separate.
- (b) Nucleus in the form of a cup and closely moulded to the capsule.

To the first two groups belong the Palinura, Astacura with exception of *Astacus*, and the Anomura, and to the second group

the Brachyura. There is no intermediate type between the Reptantia and the Natantia.

The capsule in all Anomura is ellipsoid or pyriform, while in the Palinura and Astacura it is cylindrical or spherical.

To this grouping could be added the observations of Spalding (118), who arranged the Decapoda according to their type of spermatophore and the place of spermatophore reception. In any such grouping the Thalassinidea and the Dromiidae must be omitted at present.

| | |
|-------------|--|
| Anomura. | External spermatophore reception. Pedunculate spermatophores. Capsule of spermatozoon ellipsoidal or pyriform. |
| { Palinura. | External spermatophore reception. |
| { Astacura. | Large non-pedunculate spermatophores. Capsule of spermatozoon spherical or cylindrical. |
| Brachyura. | Internal spermatophore reception. Non-pedunculate spermatophores. Capsule and nucleus of spermatozoon closely moulded. |

Biometrics of Growth and Reproduction

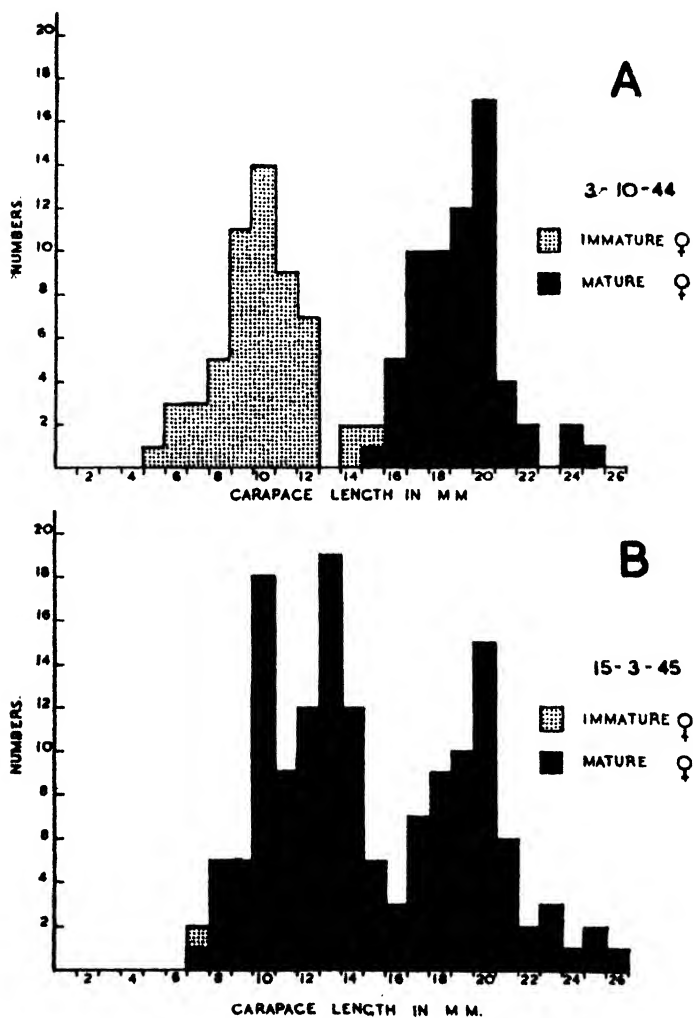
Immature females of *Galathea squamifera* can be determined by the transitional form of their pleopods (*vide* page 24) and the immature males by the lack of the male secondary sexual characters on the telson (*vide* page 27).

Unfortunately it was found impossible to collect *Galathea* in any quantity except at the equinoctial spring tides in March and October, these observations on growth rate have therefore been deduced from measurements taken only at those periods. All measurements were made from the tip of the rostrum to the median hind border of the carapace.

It will be seen that in the autumn all females with a carapace length of less than 14 mm. (Text-Fig. 12, A.) are immature, and all above this size are mature. Five months later these immature individuals have become mature and the mode of the group has shifted to the right, filling the space between the immature and

the mature groups of Text-Fig. 12, A. The mature group of Text-Fig. 12, B. has remained the same as for Text-Fig. 12, A.

GALATHEA SQUAMIFERA FROM PLYMOUTH



TEXT-FIG. 12

Carapace length measurements of *G. squamifera* collected at Plymouth in October, 1944, and March, 1945. The measurements were taken from the tip of the rostrum to the median hind border of the carapace.

Judging by the growth rates of other decapods given by Lebour (74) and Shen (114), the largest individuals of the newly-formed mature group of Text-Fig. 12, B. may be twelve months old. Zoeae of *Galathea* are found in the plankton in the South of England from January until the end of September, although they are not plentiful before March or after August. This suggests that the immature group of Text-Fig. 12, A. is four to five months old in October. By the following March this group is mature, so that maturity is reached at an average age of from nine to ten months, and so the newly-formed mature group of Text-Fig. 12, B. will have an average age of from nine to ten months.

From observations on individual specimens which have moulted in captivity, rapid growth continues up to 19 mm. carapace length, but increase in size at successive moults falls rapidly above 19 mm. This suggests that the newly-formed mature group of Text-Fig. 12, B. moves forward into the position 16-19 mm. carapace length in the next five months, giving an average age for this group of about sixteen months. Owing to the decrease in growth rate after 19 mm. carapace length, the time taken to increase from 19 mm. to 26 mm. carapace length is probably not less than twenty-four months. This would make the oldest *Galathea* over three years old and suggests an average life span of something over two years.

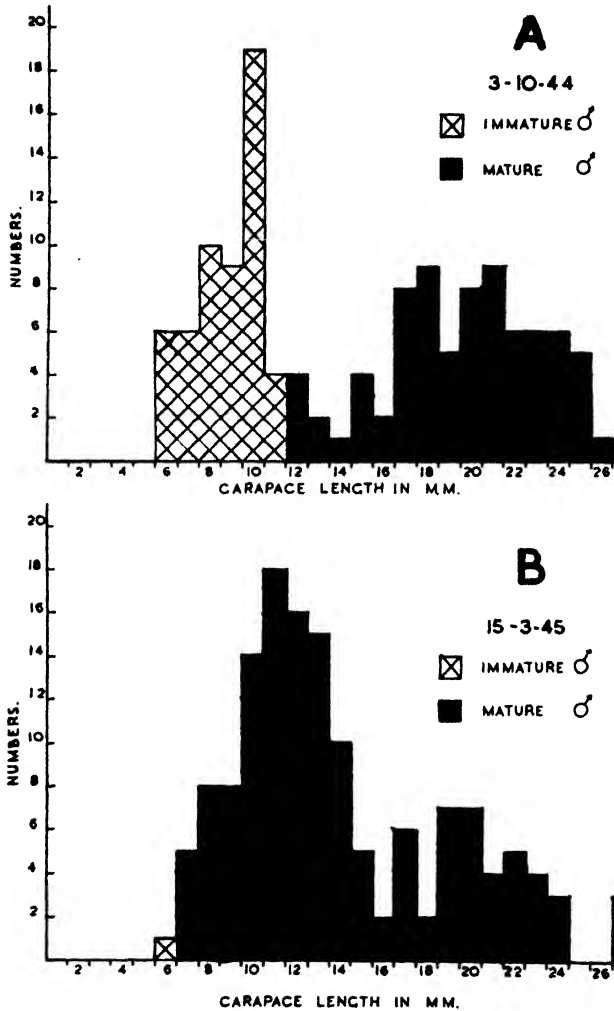
In the case of the males (Text-Fig. 13, A.B.) a similar growth rate to that of the females is shown. The young males tend to reach maturity earlier and more individuals are found of carapace length greater than 20 mm. This is probably due to an extra number of moults being possible in the males as they are not handicapped by egg laying.

Studies of the growth rate of *Cancer pagurus* by Williamson (129, 130) and Orton (93) give results of a very similar nature to those shown for *Galathea*, although the time intervals are, of course, greater.

Eggs attached to the pleopods of the right side of all size groups were counted and the number doubled to give the total. From these counts (Table page 123) the average number of eggs of individuals for each size group has been determined and Text-

Fig. 14 constructed. Only females with freshly laid eggs were used for counts, in case loss had occurred during development.

GALATHEA SQUAMIFERA FROM PLYMOUTH



TEXT-FIG. 13

Carapace length measurements of *G. squamifera* collected at Plymouth in October, 1944, and March, 1945. The measurements were taken from the tip of the rostrum to the median hind border of the carapace.

Galathea squamifera

TABLE SHOWING CARAPACE MEASUREMENT INVESTIGATIONS.

Asterisked numbers are immature female specimens.

| Date | 17.9.43. | | 26.3.44. | | 3.10.44. | | 15.3.45. | |
|---------------|----------|-----|----------|-----|----------|-----|----------|-----|
| Sex | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ |
| Length mm. | No. | No. | No. | No. | No. | No. | No. | No. |
| 5 | — | — | — | — | 1* | — | — | — |
| 6 | — | — | — | — | 3* | 6 | — | 1 |
| 7 | — | — | — | — | 3* | 6 | 2 | 5 |
| 8 | — | 3 | 1 | 1 | 5* | 10 | 5 | 8 |
| 9 | — | 5 | 5 | 3 | 11* | 9 | 5 | 8 |
| 10 | 3* | 4 | 4 | 4 | 14* | 19 | 18 | 14 |
| 11 | 3* | 2 | 19 | 7 | 9* | 4 | 8 | 18 |
| 12 | 6* | 1 | 8 | 3 | 7* | 4 | 12 | 16 |
| 13 | 4* | 4 | 7 | 11 | — | 2 | 19 | 15 |
| 14 | 3* | 1 | 7 | 4 | 2* | 1 | 12 | 10 |
| 15 | 2*+1 | 5 | 6 | 6 | 1*+1 | 4 | 5 | 5 |
| 16 | 4 | 5 | 7 | 1 | 5 | 2 | 3 | 2 |
| 17 | 8 | 8 | 2 | 4 | 10 | 8 | 7 | 6 |
| 18 | 12 | 3 | 9 | 6 | 10 | 9 | 9 | 2 |
| 19 | 9 | 7 | 1 | 3 | 12 | 5 | 10 | 7 |
| 20 | 10 | 3 | 6 | 5 | 17 | 8 | 15 | 7 |
| 21 | 7 | 6 | 3 | 4 | 5 | 9 | 6 | 4 |
| 22 | 2 | 3 | 2 | 3 | 2 | 6 | 2 | 5 |
| 23 | 1 | 10 | 1 | 3 | — | 6 | 3 | 4 |
| 24 | — | 4 | 1 | 2 | 2 | 5 | 1 | 3 |
| 25 | — | — | 3 | — | 1 | 5 | 2 | — |
| 26 | — | — | 2 | 2 | 1 | 1 | — | — |
| 27 | — | — | 1 | — | — | — | — | 3 |
| Total | 75 | 74 | 95 | 72 | 122 | 129 | 144 | 143 |

It will be seen that in every size group the actual number of eggs laid is approximately $\pm 1/3$ of the average number. This rather large variation in egg number appears also to be a common feature in *Cancer*, Williamson (129).

It has been shown previously that the majority of immature specimens become mature in nine or ten months, but only the larger sizes of this group produce more than one brood in the first season. The slope of the graph for the mature group of the first

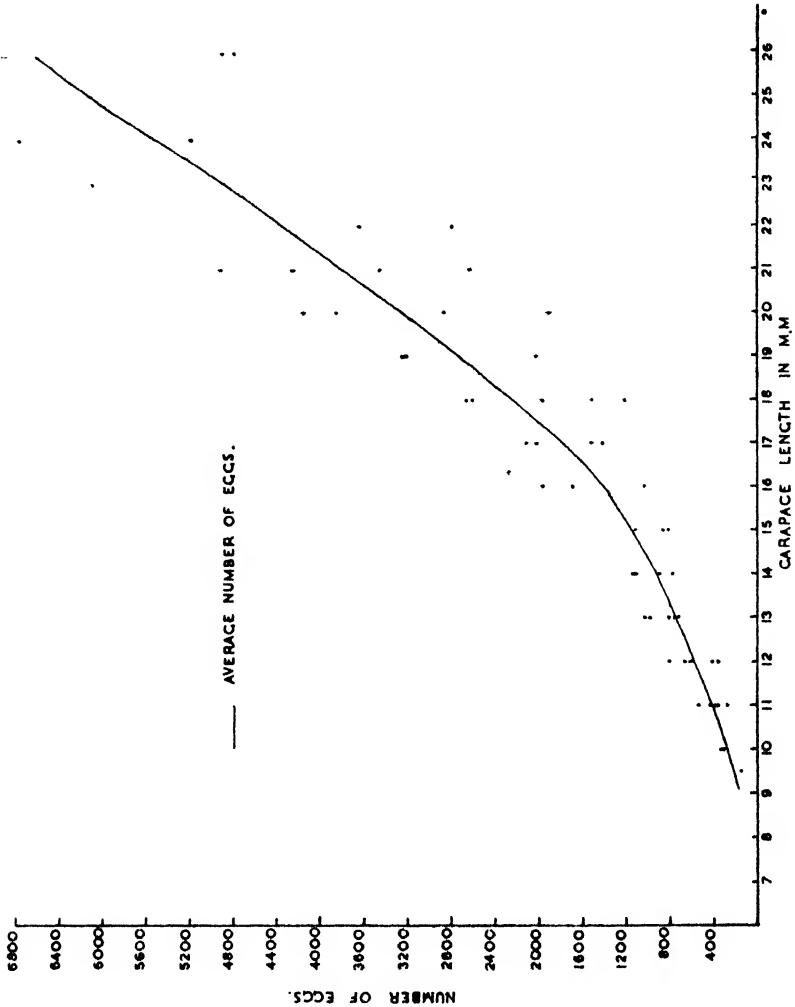
Galathea squamifera

TABLE SHOWING THE NUMBER OF EGGS IN
RELATION TO THE CARAPACE LENGTH IN MM.

| Carapace Length (mm.) | Number of Eggs. | Average. |
|-----------------------|------------------------------|----------|
| 9.5 | 160 | 160 |
| 10 | 338.328 | 333 |
| 11 | 396.435.270.376.327.554 | 393 |
| 12 | 580.406.800.368.612.660.408 | 548 |
| 13 | 984.1048.974.756.800.720.802 | 869 |
| 14 | 888.1138.1340.778 | 1038 |
| 15 | 802.864.864.1168 | 924 |
| 16 | 1032.1971.1696 | 1566 |
| 17 | 2128.2024.1510.1404 | 1766 |
| 18 | 1200.2608.2664.1534.1972 | 1995 |
| 19 | 3220.2740.3230.2020 | 2802 |
| 20 | 4162.3876.1926.2896 | 3215 |
| 21 | 4910.3474.2626.4262 | 3818 |
| 22 | 3640.2800 | 3220 |
| 23 | 6112 | 6033 |
| 24 | 6788.5200 | |
| 25 | | 5328 |
| 26 | 4800.4526 | |

season (9-16 mm. carapace length) is seen to be less than that of the second and third seasonal groups (17-26 mm. carapace length).

GALATHEA SQUAMIFERA FROM PLYMOUTH



TEXT-FIG. 14

Graph showing the average number of eggs laid by *G. squamifera* for each carapace length group.

PARASITES

Eight hundred and fifty specimens of *Galathea squamifera* were measured from Plymouth, Southern England. Of these, twelve (1·4 per cent.) were found to harbour Bopyrid parasites in the branchial chamber, with their heads pointing posteriorly with regard to the host. Rayner (109) found Bopyrids had a marked preference for the right branchial chamber in *Munida subrugosa* and *M. gregaria* from the Falkland Islands, but this preference for side was not revealed in *Galathea squamifera* from Plymouth and few of the hosts revealed any external signs of castration.

Five specimens of another isopod were obtained during dissection. These were always situated within the pericardial cavity on the left-hand side and each was pressed against the heart with its head pointing towards the posterior end of the host. No literature so far seen makes reference to an isopod in a similar position.*

Cysts varying in colour from light yellow to dark brown are usually present in the thoracic portions of the dorsal muscles, and in the flexor and extensor muscles of the pereopods. They are about the size of small pin-heads and the cyst wall is often marked with darker reticulations. Each cyst contains a single trematode parasite and *Galathea* is probably the intermediate host, with possibly a fish as the final host.

Insufficient material has been collected round the British Isles to ascertain the percentage of cyst bearing specimens in the different habitats. At Plymouth at least 90 per cent. of old specimens contain cysts.

In *Porcellana platycheles* the cysts are larger than those of *Galathea* and possess lateral wings like those of sycamore seeds.

* These are undeveloped female *Pleurocrypta galathea* (Hesse) which have somehow found their way into the pericardial cavity. (Miss N. G. Sproston personal communication.)

PART III

PALAEONTOLOGY AND DISCUSSION

Palaeontology of the Anomura

Until quite recently the existence of fossil Galatheidea was considered doubtful, but a number of fossils have now been obtained the affinity of which is certain. In the Portlandian (Upper Jurassic) several species closely related to the Galatheidea of the present day have been found and so the origin of the tribe should be sought at a period earlier than the Portlandian.

In 1854 H. von Meyer described under the name *Gastrosaccus wetzeri* a decapod crustacean found in the Lower Portlandian of Niederstotzingen, Bavaria. Since then, it, together with other species from the Upper Bathonian of Giberville (Middle Jurassic) have been found in the Coral Rag of Cambridgeshire. Straelen (120) considers that the genus *Gastrosaccus* of Meyer is a primitive member of the Galatheinae. If this is so, then the Galatheinae are pre-dated from the Upper to the Middle Jurassic.

The same author states that M. K. Segerberg has recognised the genus *Munida*, represented by one species, from the Danian of Faxø (Upper Cretaceous) and E. Loerenthey has identified the genus *Palaeomunida*, a form closely related to *Munida*, which he found in the Bathonian of Hungary (Middle Jurassic).

According to Beurlen (11) fossil remains of the chelae of Paguridea have been obtained from the Lias (Lower Jurassic), but no remains of pagurid carapaces have been found from this horizon and he thought, therefore, that these crustaceans were soft shelled. Pronounced changes in this group, however, make discussion of their relationship difficult, but he considered the similarity of the chelae to those of the Axiidae alone suggested near relationship to the Thalassinidea.

Beurlen (11) also considers that the Paguridea were derived from the Thalassinidea at a very early date and the soft carapace of the Paguridea is a legacy from the mud-boring habit of the Thalassinidea, among which a soft carapace is the general rule.

Within the Thalassinidea, however, the Axiidae are the only family that can be traced as far back as the Jurassic. Thus if the Paguridea are derived from the Thalassinidea the latter must have originated at the beginning of the Triassic.

Thus two genera of Galatheidea can be traced back to the Middle Jurassic and the Paguridea as far back as the Lower Jurassic. The earlier history of the Galatheidea is, however, unknown though Beurlen (10) has discussed their affinity with the now extinct family of Prosoponidae.

DISCUSSION

Affinities and Classification

Borradaile (15, 16), when classifying the reptant Decapoda, based his observations mainly on external characters. This has been widely accepted as the most satisfactory classification, but even so the Anomura are still held by some zoologists and palaeontologists to be an artificial group.

It may be advantageous, therefore, to see what support can be given to this classification by the study of the internal anatomy of *G. squamifera* in comparison with other Anomura and in their relationship to other Decapoda.

Owing to the divergence of external form in the Anomura it is difficult to decide whether to look upon them as having a single origin, or whether to assign to them separate points of origin arising from the Palinura and Astacura. Borradaile remarks that if a common descent is assumed for the Anomura and Brachyura, they must have divided at a very early date into two branches which soon became widely separated. One of these branches represents the Anomura and the other the Brachyura.

It seems desirable, therefore, first to try to decide whether the Anomura are a homogeneous group by a comparative study of their internal organs and then to consider what light, if any, palaeontology throws on their origin within the Decapoda.

In the foregoing sections certain organ systems were found to have a greater taxonomic value than others and these will be

discussed under the following headings, which are given in the order of their value in this respect.

- (a) The Blood System.
- (b) The Nervous System.
- (c) The Reproductive System.
- (d) The Larvae.
- (e) The Alimentary System.

Many lesser points of similarity within the group have not been mentioned, but are to be found in the summaries at the end of each section. The author has found only scanty literature on the anatomy of the Hippidea and this group has therefore not been included in the discussion.

(a) THE BLOOD SYSTEM

In the Palinura, Astacura and Brachyura there is only one main dorsal and one main ventral abdominal artery. This arrangement persists throughout the groups with minor exceptions (e.g., *Maia*, in which the ventral abdominal artery is thicker than the dorsal abdominal artery) despite the extreme reduction of the Brachyuran abdomen.

In the Anomura, on the other hand (Text-Fig. 8, page 83), the ventral abdominal artery is weak or absent and the dorsal artery, either immediately on leaving the heart, or shortly afterwards, bifurcates into two latero-dorsal arteries. This bifurcation of the dorsal abdominal artery usually occurs before the latter reaches the abdomen, but in the Thalassinidea (*Upogebia*) bifurcation does not take place until the sixth abdominal segment. The general arrangement of the abdominal arterial system in the Thalassinidea shows, however, affinities with that of the Paguridea in that the dorsal abdominal artery sends major branches to the ventral face of the abdomen where they take the place of the shortened ventral abdominal artery.

In *Dromia*, according to Bouvier (22), the dorsal abdominal artery is asymmetrical and bifurcation takes place towards the posterior boundary of the fourth abdominal segment. The ventral abdominal artery is connected with the dorsal abdominal artery by a strong branch situated in the anterior part of the abdomen ;

this arrangement he considers is in itself sufficient to differentiate *Dromia* from the rest of the Anomura. Bouvier further suggests that the general arrangement of the blood system in this genus resembles in all essentials that of typical Brachyura.

(b) THE NERVOUS SYSTEM

The variability of the nervous system in the Decapoda appears to be the result of modification in external form combined with a tendency towards coalescence in the thoracic ganglia. Since this coalescence occurs in Decapoda that maintain the caridoid facies, e.g., *Palaemon*, it seems that this represents a general tendency throughout the Decapoda and thus is likely to be of little value in comparing the affinities of the constituent groups. Attention might more profitably be directed towards variations in arrangement of the abdominal ganglia.

The most striking anomuran characteristic is the innervation of the first abdominal segment from paired ganglia fixed to the posterior end of the thoracic mass, followed by five pairs of abdominal ganglia. This arrangement remains unaltered even where the abdominal nerve chain is secondarily shortened as in *Porcellana*. Exceptions to this general arrangement are found in the Thalassinidea as according to Bouvier (17) *Axius* has six paired abdominal ganglia all within the abdomen and in *Upogebia* the first pair of abdominal ganglia although within the thorax have not yet become fixed to the thoracic mass.

In the Palinura and Astacura all six pairs of abdominal ganglia are situated within the abdomen.

In *Dromia* as described by Bouvier (19, 22) the arrangement of the thoracic and abdominal ganglia is almost identical with that of *Porcellana platycheles*.

(c) THE MALE REPRODUCTIVE SYSTEM

In the Palinura, Astacura and Brachyura the reproductive systems lie entirely within the thorax, whereas in the Anomura they may occur in the abdomen (Paguridea and Thalassinidea) or in the thorax (Galatheidea), though in some members of the latter group this system may occur entirely within the abdomen, a condition which occurs in *Petrolisthes eriomerus*, Fasten (43).

In the Palinura, Astacura and Brachyura the spermatophores are non-pedunculate while in the Anomura they are pedunculate.

In spite of the difference in position of the reproductive system in the Galatheidea and the Paguridea, the detailed structure of the male system in the two groups is closely similar, especially in the histology of the vas deferens and in the method of spermatophore formation. The reproductive system of the Thalassinidea (*Gebia*) appears to differ from any other Anomuran, but the only account seen is inadequate.

In *Dromia* the reproductive system is situated within the thorax and in external appearance closely resembles that of *Galathea*, although the two reversely wound coils are missing. The spermatophores, spermatozoa and method of fertilisation appear to conform more closely to the Brachyura.

(d) THE LARVAE

The larvae of the Galatheidea in general can only be differentiated from those of the Paguridea by a few minor characters, Gurney (54).

In the Thalassinidea, Gurney makes the interesting observation that the known larvae provide evidence of a fundamental cleavage between the Callianassinae and Upogebiinae, which are representative of two groups :

(a) Homarine Group : Axiidae and Callianassidae.

(b) Anomuran Group : Laomediidae and Upogebiidae.

This rather suggests that the homarine and anomuran groups may have arisen from the Thalassinidea.

In the Dromiacea Gurney (54) states that " In view of the uncertainty about some and the incompleteness of knowledge of other genera, only *Dromia* can safely be taken into account in considering the bearing of the larvae upon classification ".

The larva of *Dromia* has been described by Lebour (77) and she thinks that on the basis of its structure the Dromiacea must be removed from the Brachyura but that certain features make it impossible that they should belong to the Anomura. Other resemblances point to a close relationship between the ancestral dromiid and the anomuran section of the

Thalassinidea. Gurney also supports the view expressed by Lebour of an anomuran-thalassinid descent of the Dromiacea.

The larvae of the Palinura, Astacura and Brachyura are all specialised. All the Palinura have the characteristic phyllosoma larva. In the Astacura there are only three larval stages all with the same general form and according to Gurney (54) the great majority of the Brachyura have a typical zoea larva.

(e) THE ALIMENTARY SYSTEM

The fore-gut of all Reptantia differ only in detail. The features that characterise this region in the Anomura are the presence of a ridged cardio-pyloric valve, triangular plate-like lateral accessory teeth and in the filter chamber plates from the pleuropyloric valves projecting into the dorsal chamber (*vide* page 59). These plates score channels in the faecal pellets. In the Paguridea the lateral accessory teeth and the pleuropyloric plates are absent, the latter are also absent in *Munida* in the Galatheidea.

In the Palinura, Astacura and Brachyura the cardiopyloric valve is unridged, the lateral accessory teeth are usually denticulate and no plates project from the pleuropyloric valve into the dorsal chamber.

Within the Anomura the position of the digestive diverticula varies between the three groups. In the Thalassinidea and Paguridea these diverticula are mainly situated within the abdomen whereas the Galatheidea agree with the Palinura, Astacura and Brachyura in possessing digestive diverticula within the thorax. In spite of the differences in location of the diverticula within the Anomura they all show striking similarity in histological structure. This is particularly noticeable in the characteristic grouping of the gland cells (Ferment cells) upon small crests which have definite positions along the length of the tubules. This arrangement does not seem to be present in other decapods including *Dromia*.

From this discussion it would seem that the main internal organ systems in the Anomura indicate that this tribe is

homogeneous, an indication which agrees with the classification proposed by Borradaile (15, 16). Among themselves the tribes of the Anomura show closer inter-relationship than any of them show with the Palinura, Astacura and Brachyura.

The position of *Dromia* appears to be nearer to the anomuran-thalassinid stock than to the brachyuran. Cano (29) and Ortman (91) considered that the parent stem of the Dromiacea arose from a stock intermediate between the Galatheidea and the Thalassinidea, the Thalassinidea at that date being placed within the Astacura. Bouvier (22), however, considered the Dromiacea as having homarine ancestry and as having given rise to the Brachyura and this view appears to have been generally accepted. Whether the origin of the Brachyura is solved when that of the Dromiacea is accounted for now appears doubtful and Pesta (105) separates the Dromiacea from the Brachyura from which he also excludes the Oxystomata. Gurney (54) and Lebour (77) suggest an anomuran-thalassinid descent and this appears to agree best with such evidence as is presented in the above account.

From the palaeontological evidence it appears that fossil Anomura are to be found among the oldest decapod remains. There is yet no fossil evidence of the Thalassinidea occurring earlier than the Upper Jurassic, although remains of the Paguridea occur in the Lower Jurassic. If, therefore, the evidence of their primitive nature is correct the origin of the Thalassinidea must be sought in the Triassic. It appears possible, therefore, that the origin of the Reptantia could lie within a thalassinid ancestry and it may be there that the cleavage has taken place; one branch giving rise to the Palinura, Astacura and Brachyura and the other to the Anomura and Dromiacea.

From this anatomical study it is suggested that the Anomura are not an offshoot from the brachyuran stock as portrayed by Borradaile (15, 16), but have arisen independently from the parent stock. Their parentage is doubtful but it is tentatively suggested that a thalassinid ancestor is a possibility.

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PLATES

PLATE I.

- Fig. 1. *Galathea squamifera* seen from the dorsal side with the abdomen extended. (Natural size.)
- Fig. 2. *Galathea squamifera* ♀ seen from the ventral side with the thoracic appendages removed to show the articulation cavities; the pleopods of both sides have been removed. $\times 1.5$.

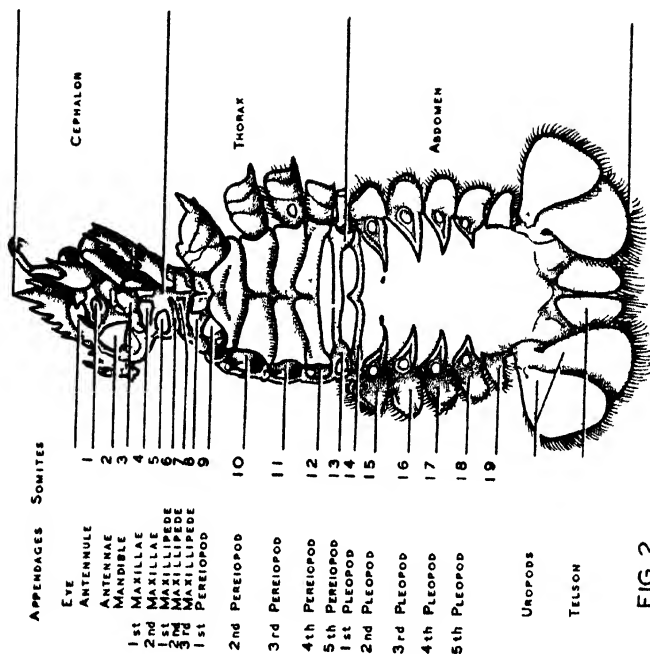


FIG 2

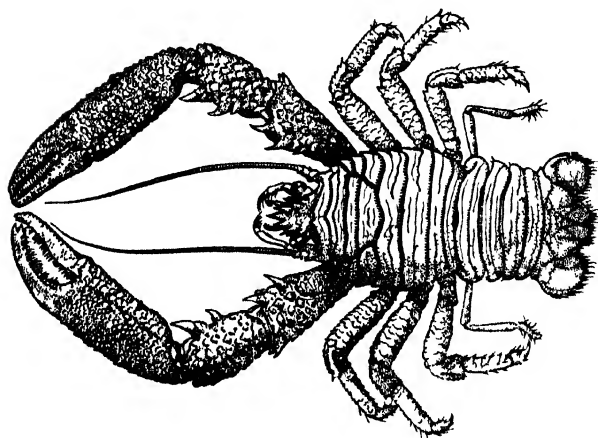


FIG 1

GALATHEA

PLATE II.

- Fig. 3. Dorsal view of rostrum, carapace and the first three terga of *G. squamifera*, to show the grooves and areas of the carapace, and the transverse grooves of the abdomen. $\times 1.75$.
- Fig. 4. Lateral view of rostrum of *G. squamifera*. $\times 4$.
- Fig. 5. Dorsal view of rostrum, carapace and the first three terga of *G. nexa*, to show the grooves and areas of the carapace, and grooves of the abdomen. $\times 2.5$.
- Fig. 6. Lateral view of rostrum of *G. nexa*. $\times 5$.
- Fig. 7. Dorsal view of rostrum, carapace and the first three terga of *G. dispersa*, to show the grooves and areas of the carapace, and the grooves of the abdomen. $\times 3$.
- Fig. 8. Lateral view of rostrum of *G. dispersa*. $\times 5$.
- Fig. 9. Lateral view to show the pleural fold, pterygostomial region of the pleural fold, grooves and areas of the carapace, and the first three segments of the abdomen of *G. squamifera*. $\times 1.75$.
- Fig. 10. Setae from the dorsal transverse grooves of the carapace of *G. squamifera*. $\times 30$.
- Fig. 11. Setae from the central border of the pterygostomial region of the pleural fold of *G. squamifera*. $\times 30$.
- Fig. 12. Pterygostomial region of *G. nexa* to show the position of blue pigment, marked in black. $\times 4.4$.
- Fig. 13. Ventral view of terga 5-6 of *G. squamifera* to show the overlapping of the anterior tergum. $\times 4$.

LETTERING

| | | | |
|--------|--------------------|---------------|--------------------------|
| ant. | = Antenna. | pl.s. | = Pleural suture. |
| cg. | = Cervical groove. | pt.r. | = Pterygostomial region. |
| fr. | = Facial region. | terg. 1-3 | = Terga 1 to 3. |
| gr. | = Gastric region. | terg. 4, 5, 6 | = Terga 4 to 6. |
| hr. | = Hepatic region. | tr. | = Thoracic region. |
| pl.1-3 | = Pleura 1 to 3. | | |

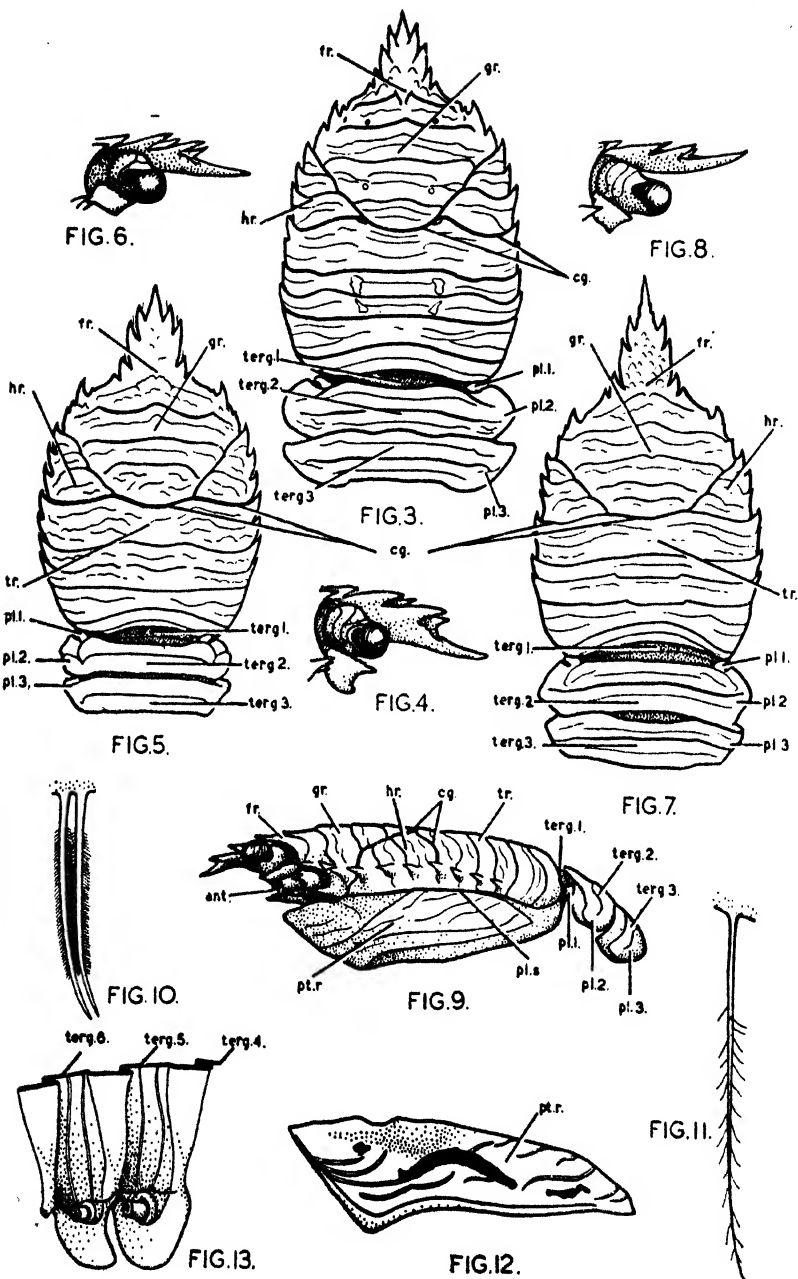


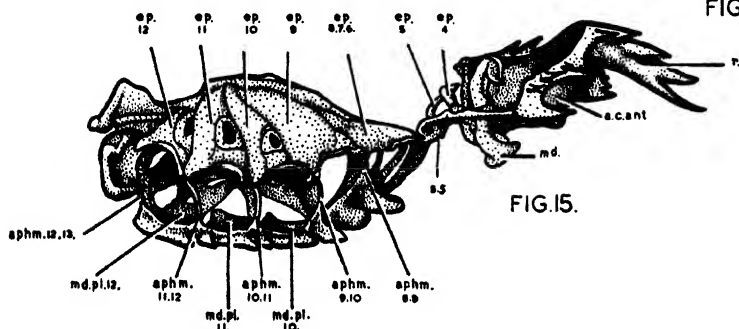
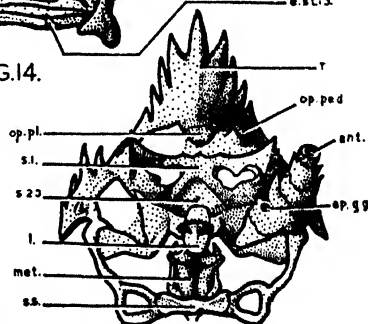
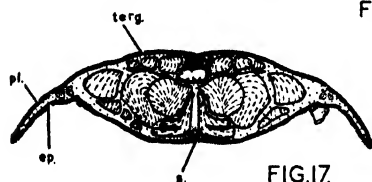
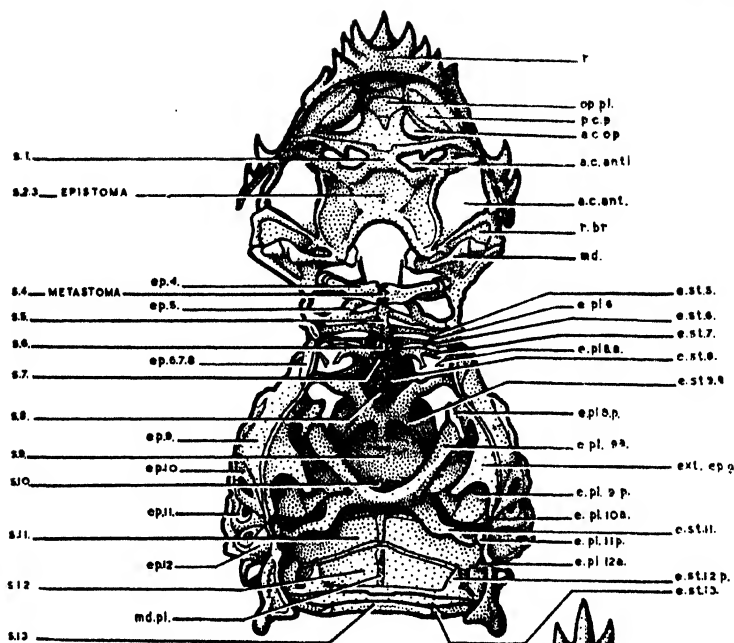
PLATE III.

G. squamifera.

- Fig. 14. The Cephalothoracic Endophragmal System seen from the dorsal side. The Carapace and all soft parts have been removed. $\times 3$.
- Fig. 15. The Cephalothoracic Endophragmal System seen from the right hand side. The Carapace and all soft parts have been removed. $\times 3$.
- Fig. 16. The Cephalon seen from the ventral side. All soft parts have been removed except the Optic Peduncle (op. ped.), Antenna (ant.), Labrum (l.), and Metastoma (met.). $\times 3$.
- Fig. 17. Transverse section through the second Abdominal segment showing the general structure. $\times 3$. Diagrammatic.

LETTERING

| | | | |
|-----------|--------------------------------------|---------|--|
| a.c.ant. | = Articular cavity of the Antenna. | l. | = Labrum. |
| a.c.antl. | = Articular cavity of the Antennule. | md. | = Mandible. |
| a.c.op. | = Optic articular cavity. | md.pl. | = Median plate for Somites 10, 11, 12. |
| ap.g.g. | = Aperture for the antennary gland. | met. | = Metastoma. |
| ant. | = Antenna. | op.ped. | = Optic peduncle. |
| aphm. | = Arthrophragm between Somites 8-13. | op.pl. | = Optic plate. |
| ep. | = Epimera 4-12. | p.c.p. | = Pro-cephalic process. |
| e.pl. | = Endopleurite 6-12. | pl. | = Pleura. |
| | a = anterior plate. | r. | = Rostrum. |
| | p = posterior plate. | r.br. | = Roof of the pre-branchial chamber. |
| e.st. | = Endosternite 5-13. | s. | = Sternum 1-13. |
| ext.ep.9 | = Extension of the 9th Epimera. | terg. | = Tergum. |



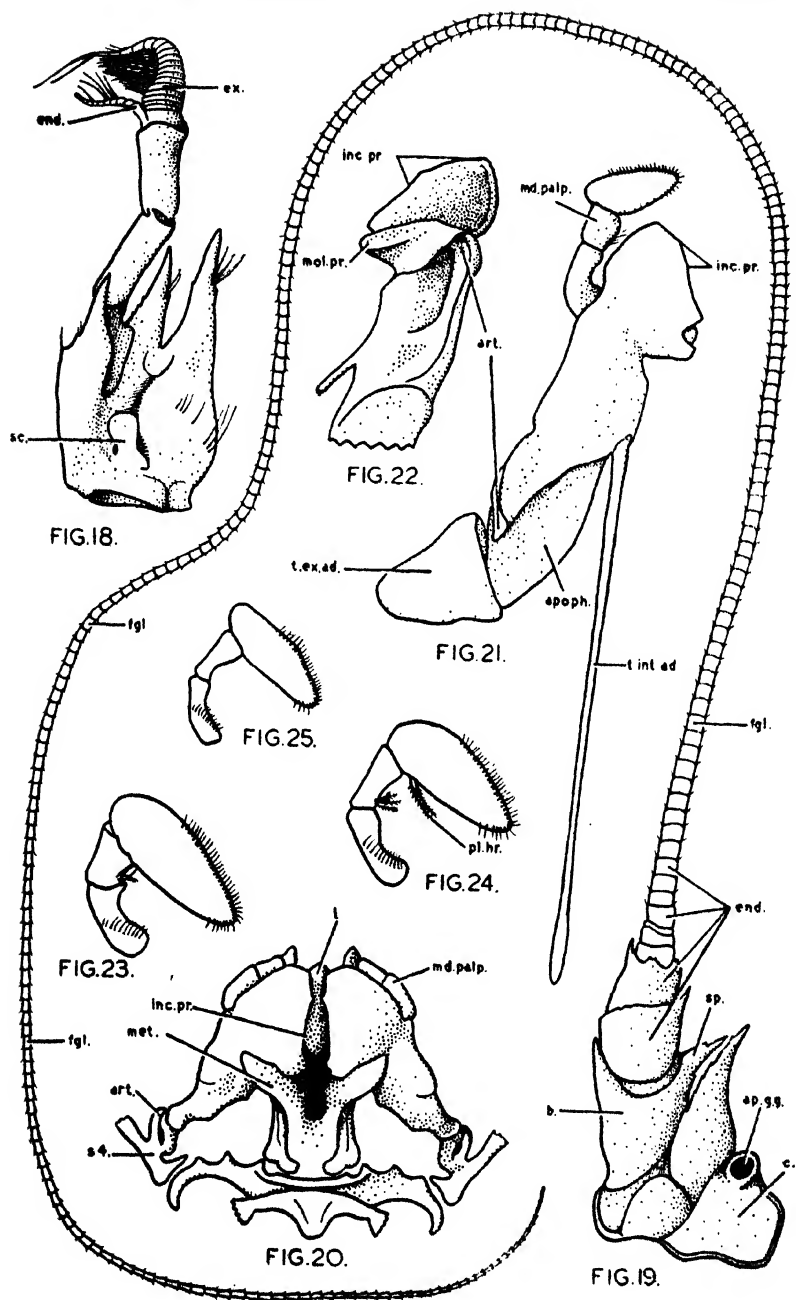
GALATHEA

PLATE IV.

- Fig. 18. Antennule of right side of *G. squamifera* seen from the dorsal surface. $\times 8$.
- Fig. 19. Antenna of right side of *G. squamifera* seen from the ventral surface. $\times 8$.
- Fig. 20. Mandibles of *G. squamifera* in natural position seen from the ventral surface. It shows articulation (art.) with the fourth sternum (s4.), the labrum (l), the mandibular palps (md. palp.) and the metastoma (met.). $\times 6$.
- Fig. 21. Mandibles of the right side of *G. squamifera*, dissected out and seen from the ventral surface, the apophysis (apoph.), the tendons (t. ex.ad t.int.ad.), and the mandibular palps (md.palp.). $\times 15$.
- Fig. 22. Mandibles of the right side of *G. squamifera* dissected out to show the dorsal surface, the concave anterior portion, and the articulation (art.) of the dorsal surface. $\times 15$.
- Fig. 23. Mandibular palps of *G. squamifera*, right hand side ventral surface. $\times 10$.
- Fig. 24. Mandibular palps of *G. dispersa*, right hand side ventral surface after Bull. $\times 10$.
- Fig. 25. Mandibular palps of *G. nexa*, right hand side ventral surface after Bull. $\times 10$.

LETTERING

| | | | |
|----------|---|-----------|---|
| ap.g.g. | = Aperture for the duct of the antennary gland. | met. | = Metastoma. |
| apoph. | = Apophysis. | mol.pr. | = Molar process. |
| art. | = Articulation. | pl.hr. | = Plumose setae. |
| b. | = Basis. | s4. | = 4th Sternum. |
| c. | = Coxa. | sc. | = Scale. |
| end. | = Endopod. | sp. | = Spine. |
| ex. | = Exopod. | t.ex.ad. | = Tendon for the attachment of the external adductor muscles. |
| fgl. | = Flagellum. | t.int.ad. | = Tendon for the attachment of the internal adductor muscles. |
| inc.pr. | = Incisor process. | | |
| l. | = Labrum. | | |
| md.palp. | = Mandibular palps. | | |



GALATHEA

PLATE V.

G. squamifera.

- Fig. 26. First maxilla of the right hand side ventral view. $\times 10$.
- Fig. 27. Coxa of first maxilla with the chitin of the ventral lamina removed showing the skeletal support (skel.), and immediately below this the cut edge of its attachment to the body. $\times 10$.
- Fig. 28. Seta from the apex of the coxa of the first maxilla showing serrated apex. $\times 70$.
- Fig. 29. Second maxilla right hand side ventral view. $\times 10$.
- Fig. 30. First maxilliped right hand side ventral view. $\times 10$.
- Fig. 31. Second maxilliped right hand side ventral view. $\times 8$.
- Fig. 32. Third maxilliped right hand side ventral view. $\times 5$.
- Fig. 33. Serrated setae from the dactylus (d. Fig. 32) of the third maxilliped, showing single row of teeth. $\times 35$.
- Fig. 34. Setae from the lateral border of the merus (m.) carpus (c') and propodus (p.) of the third maxilliped Fig. 32. $\times 15$.

LETTERING

| | | | |
|------|-------------|-------|---------------------|
| b. | = Basis. | fgl. | = Flagellum. |
| c. | = Coxa. | i. | = Ischium. |
| c'. | = Carpus. | m. | = Merus. |
| d. | = Dactylus. | p. | = Propodus. |
| end. | = Endopod. | pr. | = Praecoxa. |
| epi. | = Epipod. | scap. | = Scaphognathite. |
| ex. | = Exopod. | skel. | = Skeletal support. |
| ext. | = Exite. | | |

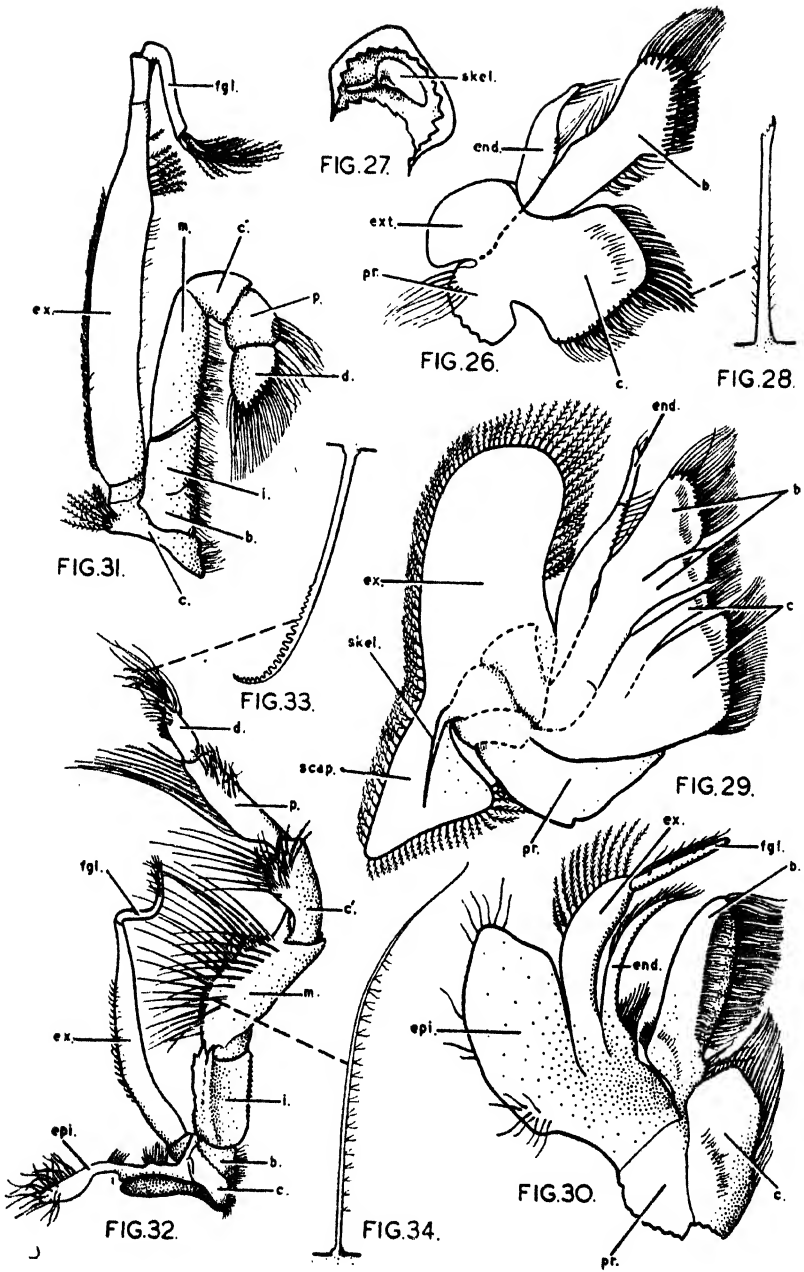


PLATE VI.

G. squamifera.

- Fig. 35. First pereopod, or chela, seen from the dorsal view. The scales are not shown in the drawing, but may be seen in Fig. 1. $\times 2$.
- Fig. 36. First pereopod, or chela, showing longitudinal section of Fig. 35. with tendons t.fl. 1-6, and t.ex 1-6, and the disarticulation at the fracture plane. $\times 2$.
- Fig. 37. Magnified view of dorsal articulation between propodus (p.) and carpus (c.) of Fig. 36.
- Fig. 38. Ventral view of first pereopod, or chela, showing the interlocking spurs i.sp.1. and i.sp.2. The fracture plane (f.p.), and sternum (s.). $\times 3$.
- Fig. 39. Third pereopod seen from the dorsal side. $\times 2$.
- Fig. 40. Third pereopod seen from the dorsal side, longitudinal section, with tendons t.fl. 1-6, and t.ex 1-6. $\times 2$.
- Fig. 41. Fifth pereopod showing general view with setae dactylus (d.) and propodus (p.), and the opening for the vas deferens (vd.o.). $\times 2$.
- Fig. 42. Shows the sickle shaped setae from the propodus (p. Fig. 41) with teeth (t.) along the concave margin. $\times 10$.
- Fig. 43. Shows a small sector of Fig. 42 looking at the concave margin with the double row of teeth (t.). $\times 300$.

LETTERING

| | | | |
|---------|------------------------|-----------|---|
| b. | = Basis. | p. | = Propodus. |
| c. | = Coxa. | sj. | = Socket joint. |
| c'. | = Carpus. | t. | = Teeth on sickle shaped setae. |
| d. | = Dactylus. | t.ex. 1-6 | = Tendon for attachment of extensor muscle 1-6. |
| epi. | = Epipod. | t.fl. 1-6 | = Tendon for attachment of flexor muscle 1-6. |
| f.p. | = Fracture plane. | vd.o. | = Opening of the vas deferens. |
| i. | = Ischium. | | |
| i.sp.1. | = Interlocking spur 1. | | |
| i.sp.2. | = Interlocking spur 2. | | |
| m. | = Merus. | | |

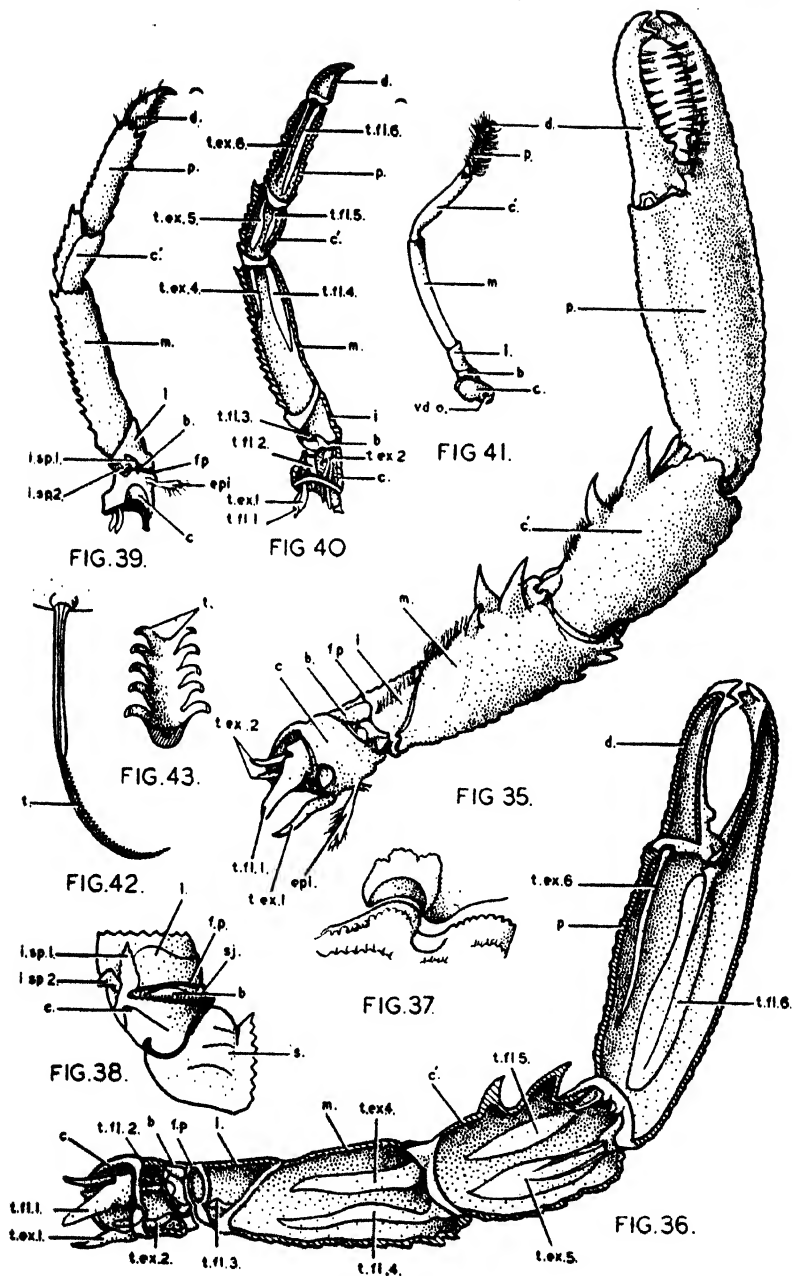


PLATE VII.

- Fig. 44. First Pleopod right hand side of male *G. squamifera* lateral view. $\times 10$.
- Fig. 45. First Pleopod right hand side of male *G. squamifera* mesial view. $\times 10$.
- Fig. 46. Second Pleopod right hand side of male *G. squamifera*, posterior view. $\times 10$.
- Fig. 47. First and second Pleopods of male, right hand side, with the endopods separated. $\times 10$.
- Fig. 48. Third Pleopod right hand side of male *G. squamifera*. $\times 10$.
- Fig. 49. A single segment of the distal portion of the plumose setae of the male basis. $\times 250$.
- Fig. 50. Fifth pleopod right hand side of male *G. squamifera* showing deformity. $\times 10$.
- Fig. 51. Inter-sexual stage of pleopod of immature female *G. squamifera*. $\times 30$.
- Fig. 52. Third pleopod of mature female of *G. squamifera*. $\times 6$.
- Fig. 53. Uropod right hand side of *G. squamifera*. $\times 5$.

LETTERING

| | | | |
|------|-------------------|------|------------|
| b. | = Basis. | end. | = Endopod. |
| b.2. | = Reversed basis. | ex. | = Exopod. |
| c. | = Coxa. | sym. | = Sympod. |

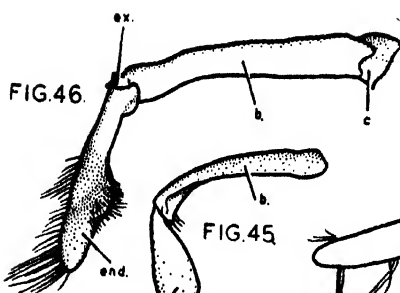


FIG. 46.

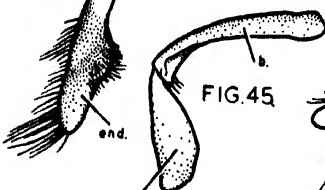


FIG. 45.

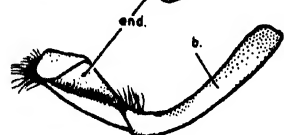


FIG. 44.

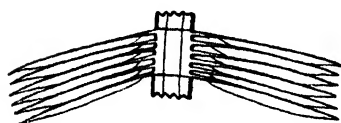


FIG. 49.

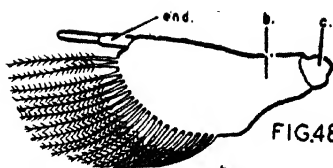


FIG. 48.

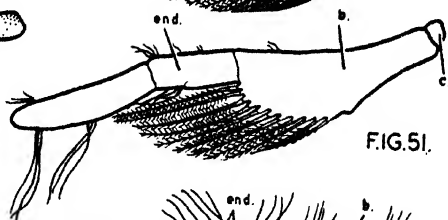


FIG. 51.

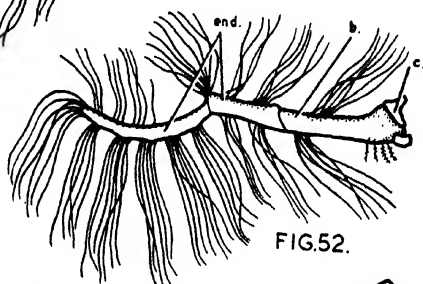


FIG. 52.

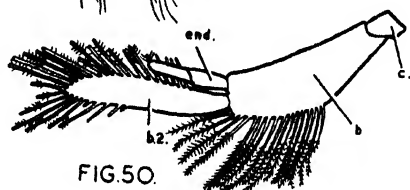


FIG. 50.

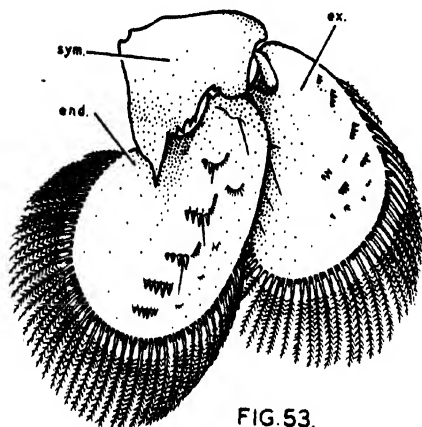


FIG. 53.

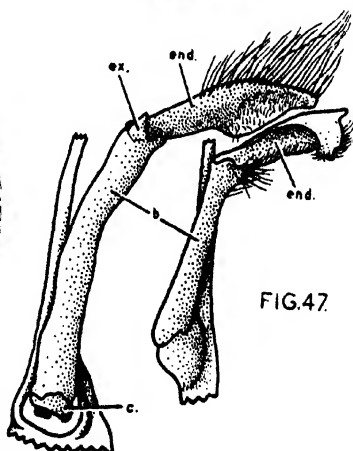


FIG. 47.

PLATE VIII.

- Fig. 54. Dorsal view of telson of male *G. squamifera*, showing the position of the plates, scales, and the male characters on the free margin of the lateral plate (ltr.pl.). $\times 10$.
- Fig. 55. Dorsal view of telson of female *G. squamifera* showing the position of the plates, scales, and female characters on the free margin of the lateral plate (ltr.pl.). $\times 10$.
- Fig. 56. Dorsal view of right half of telson of male *G. nexa*, showing the position of plates, scales and male characters on the free margin of the lateral plate (ltr.pl.). $\times 12$.
- Fig. 57. Dorsal view of left half of telson of male *G. dispersa*, showing position of plates, scales and the male characters on the free margin of the lateral plate (ltr.pl.). $\times 12$.
- Fig. 58. Showing the plumose and non plumose setae bordering the scales of *G. squamifera*. $\times 100$.
- Fig. 59. Showing the plumose and non plumose setae bordering the scales of *G. nexa*. $\times 100$.
- Fig. 60. Showing the plumose and non plumose setae bordering the scales of *G. dispersa*. $\times 100$.
- Fig. 61. Anterior half of pleuron of male *G. squamifera* seen from the ventral mesial face, showing a single irregular row of attachment scars (att. scr.) of the plumose setae. $\times 45$.
- Fig. 62. Anterior half pleuron of female *G. squamifera* seen from the ventral mesial face, showing five or six irregular rows of attachment scars (att. scr.) of the plumose setae. $\times 45$.
- Fig. 63. Fifth abdominal pleuron of male *G. squamifera* seen from the mesial face, with a single row of plumose setae. $\times 25$.
- Fig. 64. Fifth abdominal pleuron of female *G. squamifera* seen from the ventral mesial face, showing longer plumose setae in two rows at the distal end. $\times 25$.

LETTERING

ant.ltr.pl. = Antero-lateral plate of
telson.
att.scr. = Attachment scars of
setae to pleuron.
cent.pl. = Central plate of telson.

int.pl. = Intermediate plate of
telson.
ltr.pl. = Lateral plate of telson.
med.pl. = Median plate of telson.
post.pl. = Posterior plate of telson.

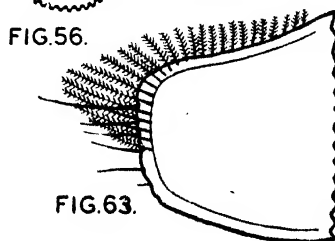
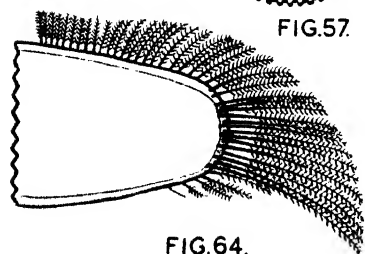
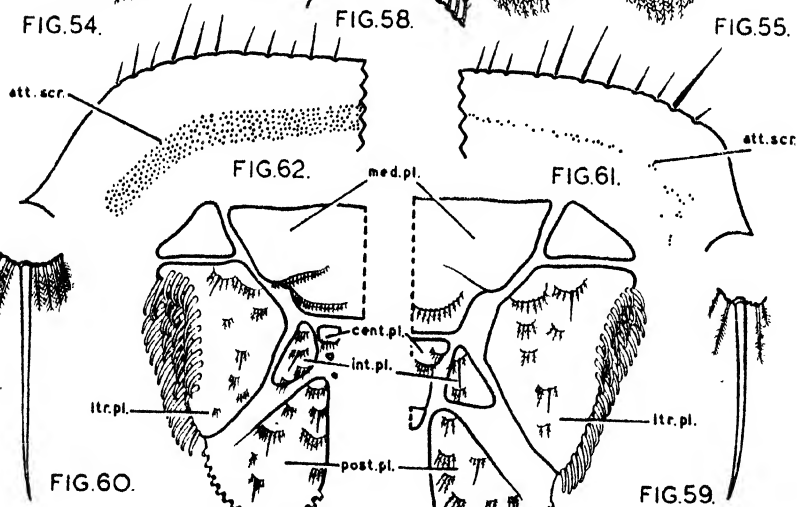
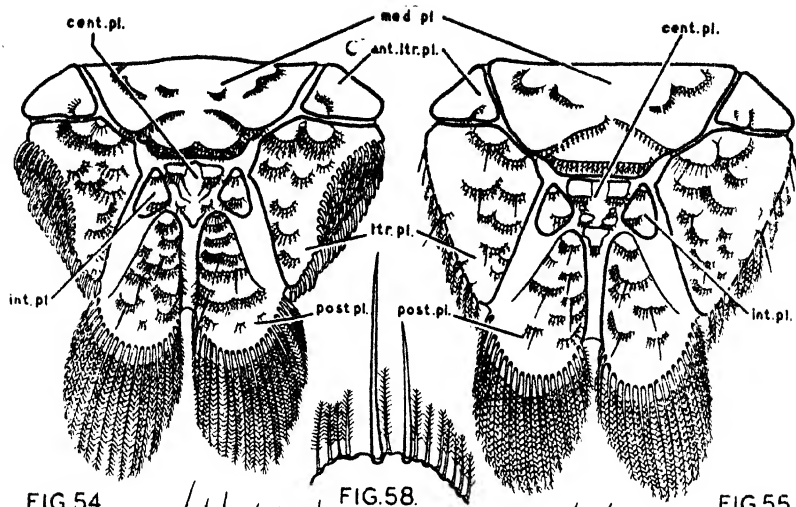
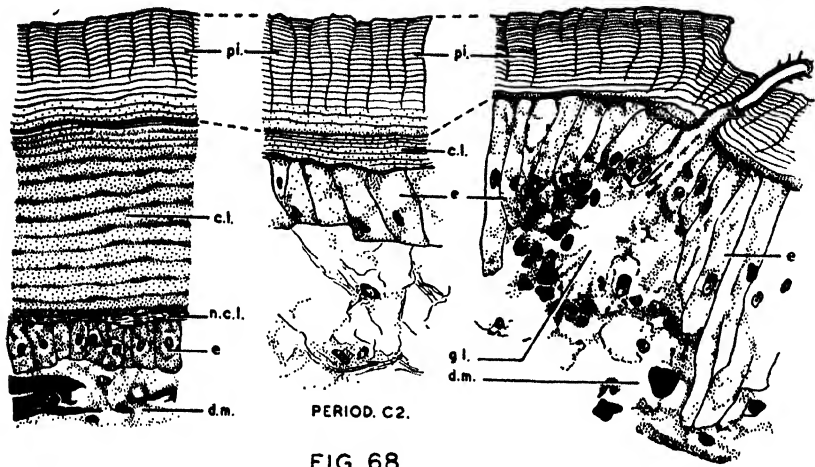


PLATE IX.

- Fig. 65. Transverse section through the fully formed carapace of *G. squamifera*. The cuticle is absent or extremely thin. Vertical divisions seen in the pigmented layer (pi.). The epidermal cells are short. $\times 500$.
- Fig. 66. Horizontal section through the carapace, pigmented layer, of *G. squamifera*. This shows the cellular derivation of the layer. $\times 500$.
- Fig. 67. Transverse section through the carapace of a freshly moulted *G. squamifera*. A gland at the base of a sensory seta is seen below the pre-exuvial pigmented layer. The epidermal cells (e) are extremely long. $\times 500$.
- Fig. 68. Transverse section through a recently moulted *G. squamifera* showing the commencement of the calcified layer (c.l.) and the reduction in length of the epidermal cells. $\times 500$.
- Fig. 69. Transverse section through the old carapace of *G. squamifera* showing the absorption of the calcified layer prior to moulting. $\times 500$.
- Fig. 70. Tegumental glands from the oesophagus of *G. squamifera* showing the basal nuclei (n.t.gl.) and the main central duct. (d.t.gl.). $\times 600$.
- Fig. 71. Longitudinal section through the basis of the female pleopod of *G. squamifera* showing tegumental glands (t.gl.) and their ducts passing up the leg to the setae. $\times 50$.

LETTERING

| | | | |
|---------|-----------------------------|---------|--------------------------------|
| c.l. | = Calcified layer. | n.c.l. | = Non-calcified layer. |
| d.m. | = Dermis. | n.t.gl. | = Nucleus of tegumental gland. |
| d.t.gl. | = Duct of tegumental gland. | pi. | = Pigmented layer. |
| e. | = Epidermis. | pl.n. | = Nerve to pleopod. |
| gl. | = Gland. | t.gl. | = Tegumental gland. |
| ly. | = Lymph. | | |



PERIOD. C4.
FIG. 65.

PERIOD. A1.
FIG. 67

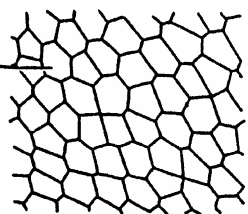
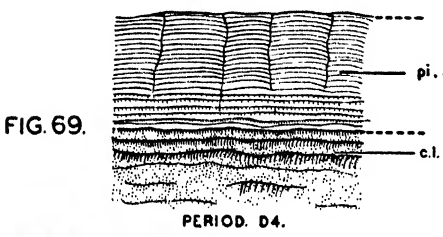


FIG. 66.

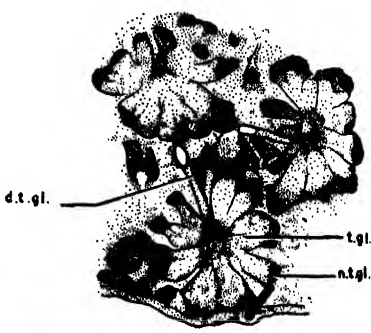
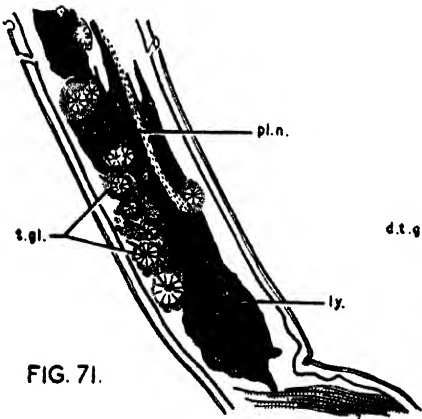


FIG. 70.

PLATE X.

- Fig. 72. Ventral view of abdomen of *G. squamifera*. The right hand side shows the muscles in their untouched positions. The first three segments of the left hand side have the thoracico-abdominal and the anterior oblique muscles removed to expose the transverse and posterior oblique muscles. The last three abdominal segments also have the posterior oblique muscles removed to expose further the central and transverse muscles. $\times 5$.
- Fig. 73. Lateral dissection from the median line of left side of *G. squamifera*. The anterior oblique muscles have been removed to show the central, posterior oblique and transverse muscles. $\times 5$.
- Fig. 74. Same as for Fig. 73, with the additional removal of the central, transverse and posterior oblique muscles. The auxiliary and external arms of the anterior oblique muscles are exposed. The dotted lines continue the anterior oblique muscles to their attachment to the corresponding external arm. $\times 5$.

LETTERING

| | | | |
|------------|--|------------|---|
| ra-1b. | = Thoracico-abdominal muscles. | viiA-viiE. | = Transverse muscles. |
| iiA-iiF. | = Anterior oblique muscles. | m.fl.1 | = Flexor muscle of coxa of chela, somite 9. |
| iiiA-iiiD. | = Posterior oblique muscles. | m.fl.2 | = Flexor muscle for basis of chela, somite 9. |
| ivb-ivf. | = External arm of the anterior oblique muscle. | m.fl.2 | = Flexor muscles for basis of pereopods. |
| vb-vg. | = Auxiliary muscles to the anterior oblique muscles. | 10, 11, 12 | = Somites 10, 11, 12. |
| via-vif. | = Central muscles. | | |

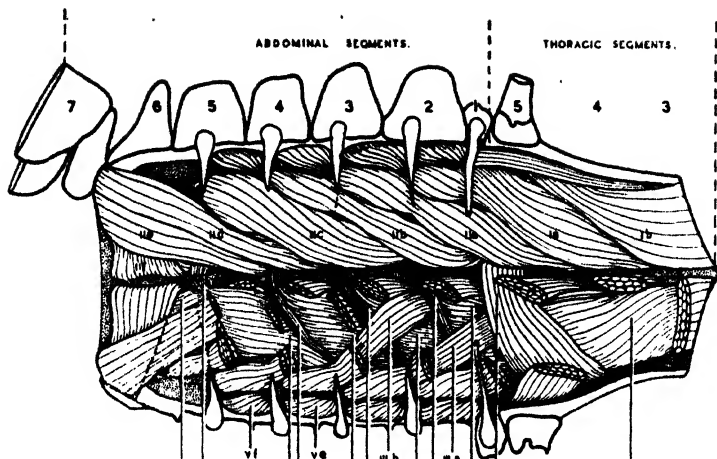


FIG. 72.

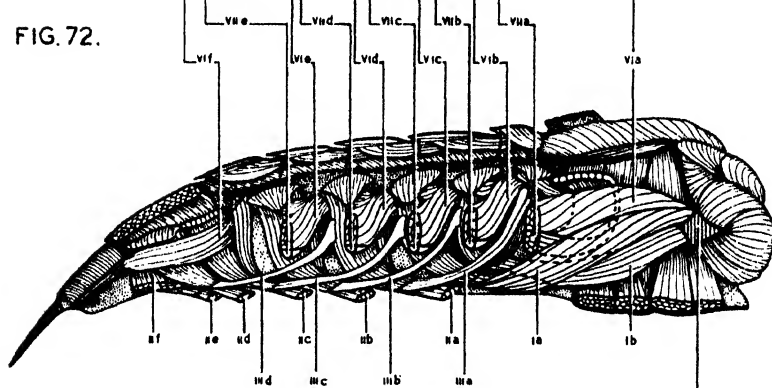


FIG. 73.

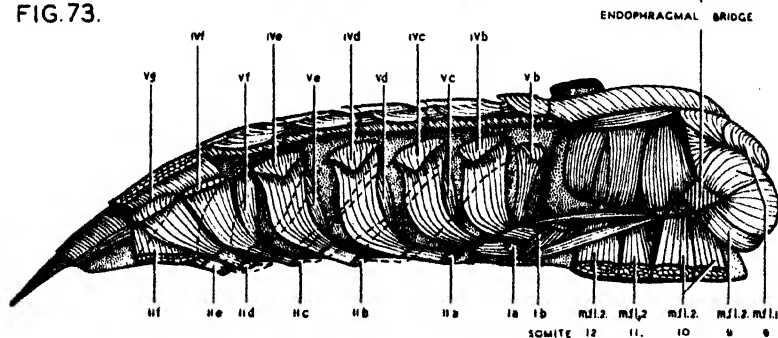


FIG. 74.

PLATE XI.

- Fig. 75. Lateral dissection from the median line of *G. squamifera*. The anterior portion shows the near side attachments of the mandibular, antennary and gastric muscles. The digestive diverticula have been removed. $\times 3.5$.
- Fig. 76. Dorsal dissection of *G. squamifera* to show the dorsal extensor muscles. The gastric mill and the digestive diverticula have been removed to reveal the underlying muscles. $\times 3.5$.
- Fig. 77. Superficial ventral muscles of the thorax of *G. squamifera* seen from the dorsal side. This also includes the first three abdominal segments with the abdominal superficial ventral muscles. The ventral nerve chain overlies all these muscles. $\times 6$.
- Fig. 78. Dorsal view of telson of *G. squamifera* to show the muscles of the tail lobe, telson and uropods. $\times 5$.

LETTERING

| | | | |
|-------------|--|--------------|---|
| a.g.m. | = Anterior gastric muscle. | l.th.m. | = Outer lateral thoracic muscle. |
| ab.m.m. | = Abductor muscle of mandible. | m.d.m.1,2,3 | = Main dorsal muscles. |
| ab.m.u. | = Abductor muscle of uropod. | m.d.s.m. | = Median dorsal superficial muscles. |
| ab.s.v.m.1 | = Median abdominal superficial ventral muscles. | m.fl.2. | = Flexor muscle of basis for pereopods 10, 11. |
| ab.s.v.m.2 | = Lateral abdominal superficial ventral muscles. | p.l.d. | = Posterior lateral dilator muscles of oesophagus. |
| ab.t.s.v.m. | = Transverse superficial ventral muscle. | p.m. | = Posterior muscle of telson |
| ad.m.m. | = Adductor muscle of mandible. | t.int.ad. | = Tendon for internal adductor muscle. |
| ad.m.u. | = Adductor muscle of uropod. | th.s.v.m.1,2 | = Lateral thoracic superficial ventral muscles. |
| ant.ex.m. | = Extensor muscle of antenna. | v.m.t. | = Ventral muscle of telson. |
| ant.fl.m. | = Flexor muscle of antenna. | 1a-1b. | = Thoracico-abdominal muscles. |
| end. | = Endopod. | 11a-11f. | = Anterior oblique muscles. |
| ex. | = Exopod. | 1vb-1vf. | = External arm of the anterior oblique muscles. |
| ex.m.t.l. | = Extensor muscle of tail lobe. | vi. | = Modified auxiliary muscle to the anterior oblique muscle. |
| f.m.t. | = Flexor muscle of telson. | vii-a-vii.e. | = Combined central and transverse muscle. |
| f.m.t.l. | = Flexor muscle of tail lobe. | | |
| i.p.g. | = Internal posterior gastric muscle. | | |

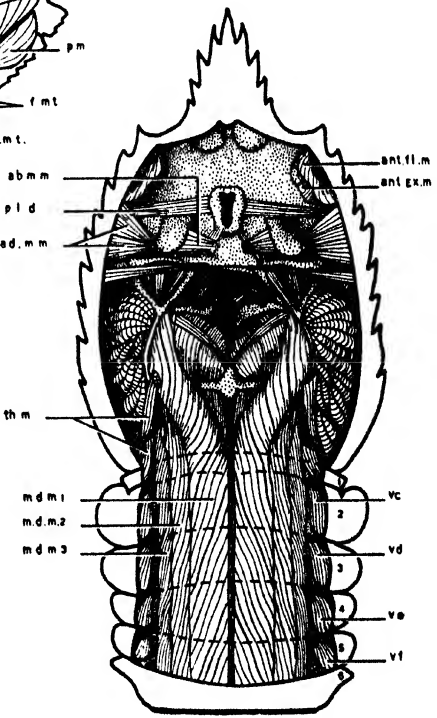
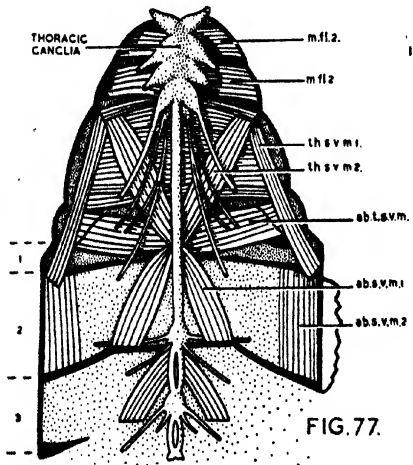
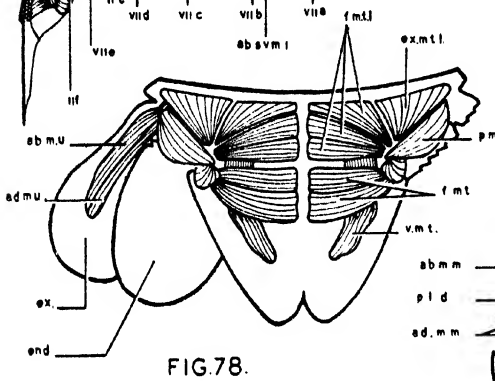
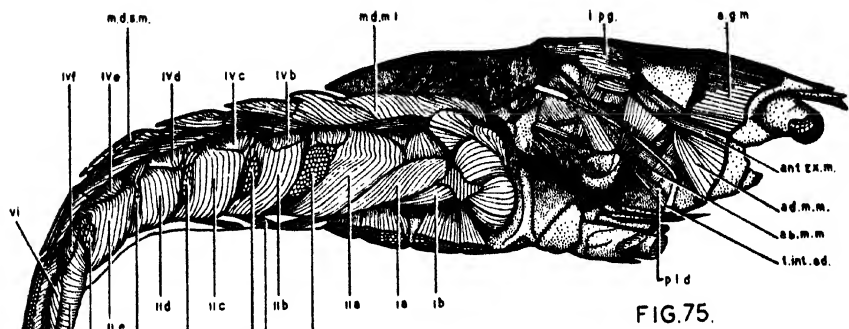


PLATE XII.

- Fig. 79. Ossicles of the fore-gut of *G. squamifera* seen from the side. The ossicles are marked in black and the chitinous wall of the stomach is stippled. $\times 7$.
- Fig. 80. Ossicles of the fore-gut of *G. squamifera* seen from the dorsal aspect. $\times 6$.
- Fig. 81. Ossicles of the fore-gut of *G. squamifera* seen from the ventral aspect. $\times 4$.
- Fig. 82. Vertical longitudinal section through the fore-gut of *G. squamifera* showing the gastric armature, valves and food channels. $\times 7$.

LETTERING

| | | | |
|---------|--|----------|---|
| a.i.p. | = Antero-inferior pyloric ossicle. | m.t. | = Median tooth. |
| a.m. | = Anterior mesopyloric ossicle. | p.a. | = Pyloric ampulla. |
| a.pl. | = Anterior pleuropyloric ossicle. | p.cd.pl. | = Postero-lateral cardiac plate. |
| c.p.v. | = Cardio-pyloric valve. | p.m. | = Posterior mesopyloric ossicle. |
| cd.pl. | = Cardiac plate of fore-gut. | p.pec. | = Pre-pectineal ossicle. |
| d.v. | = Dorsal valve of pyloric stomach. | p.pl. | = Posterior pleuropyloric ossicle. |
| ex.py. | = Exopyloric ossicle. | pl.v. | = Pleuropyloric valve. |
| i.l. | = Infero-lateral cardiac ossicle. | pr.p. | = Prepyloric ossicle. |
| l.a.t. | = Lateral accessory tooth. | pt.c. | = Pterocardiac ossicle. |
| l.oe.v. | = Lateral oesophageal valve. | pt.pec. | = Post-pectineal ossicle. |
| l.t. | = Lateral tooth. | py. | = Pyloric ossicle. |
| l.v. | = Lateral valve of the pyloric fore-gut. | s.dt. | = Subdentary ossicle. |
| l.v.v. | = Lower ventral valve of the pyloric fore-gut. | u.c. | = Urocardiac ossicle. |
| m.c. | = Mesocardiac ossicle. | u.p. | = Uropyloric ossicle. |
| m.pl. | = Middle pleuropyloric ossicle. | v.g. | = Ventral groove. |
| | | v.t.v. | = Ventral terminal valve of pyloric fore-gut. |
| | | v.v. | = Ventral valve of pyloric fore-gut. |
| | | z.c. | = Zygocardiac ossicle. |

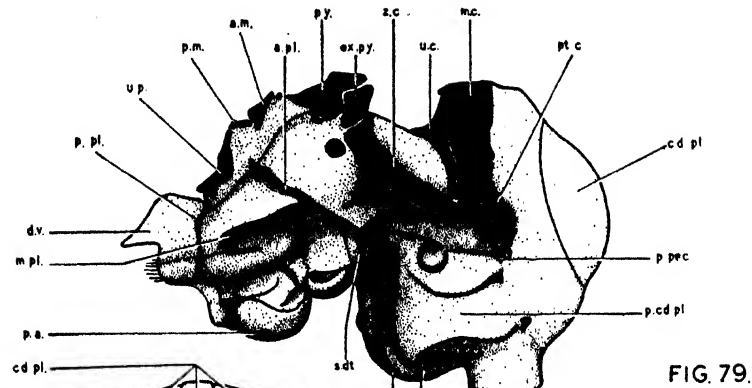


FIG. 79.

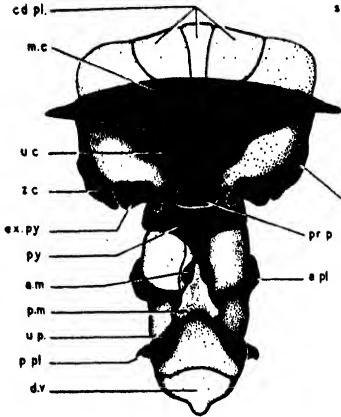


FIG. 80.

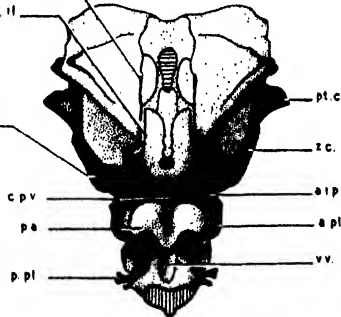


FIG. 81.

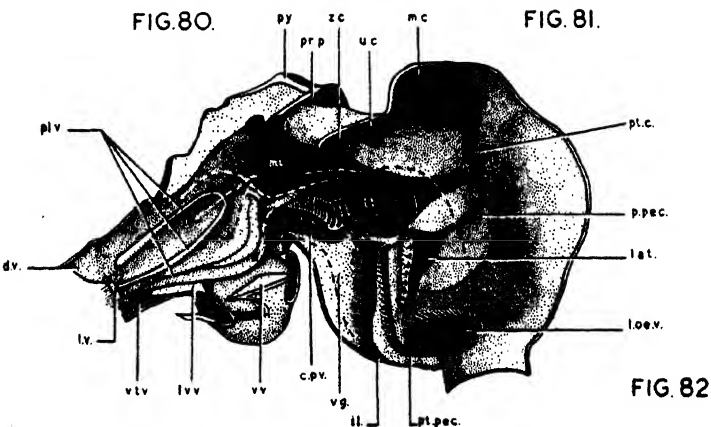


FIG. 82.

PLATE XIII.

- Fig. 83. Lateral view of the fore-gut of *G. squamifera* showing the extrinsic and intrinsic muscles of the cardiac and pyloric stomach. $\times 7$.
- Fig. 84. Dorsal view of the fore-gut of *G. squamifera*. The right half of the anterior gastric muscle (a.g.m.) has been removed to reveal the underlying muscle. $\times 4$.
- Fig. 85. Cross section of a tubule of the digestive diverticulum of *G. squamifera* showing the disposition of gland cells (g.c.) and absorptive cells (a.c.). A small portion of the adjacent tubule is seen on the lower side. $\times 100$.
- Fig. 86. Gland cells of digestive diverticula of *G. squamifera* showing the basally situated nuclei above which are vacuoles filled with granular contents and capped with a double striated border. $\times 350$.
- Fig. 87. Absorptive cells of the digestive diverticula of *G. squamifera* showing the fat globules (f.gb.) and striated border. The granular cells (gr.c.) are also shown without fat and having a single vesicle above the nucleus. An inclusion may be seen in the vesicle. $\times 600$.

LETTERING

| | | | |
|---------|--|-----------|---|
| a.c. | = Absorptive cell. of digestive diverticula. | i.py.d. | = Inner pyloric dilator muscle. |
| a.g.m. | = Anterior gastric muscle. | l.a.d. | = Lower anterior dilator muscle. |
| b.m. | = Basal membrane | l.c. | = Lateral cardiac muscle. |
| b.v. | = Blood vessel. | l.d.py.d. | = Latero-dorsal pyloric dilator muscle. |
| c.c.m. | = Cardiac constrictor muscle. | l.o.e.d. | = Lateral oesophageal dilator muscle. |
| c.o.e. | = Circular muscle of oesophagus. | l.py. | = Lateral pyloric muscle. |
| c.py. | = Cardio-pyloric muscle. | o.py.d. | = Outer ventral pyloric dilator muscle. |
| c.t. | = Connective tissue. | p.l.d. | = Postero-lateral dilator muscle. |
| d.py.d. | = Dorsal pyloric dilator muscle. | p.o.e.d. | = Posterior oesophageal dilator muscle. |
| e.p.g. | = External posterior gastric muscle. | rp.c. | = Replacement cells. |
| f.gb. | = Fat globules of absorptive cells. | t.c. | = Cavity of tubule of digestive diverticulum. |
| g.c. | = Gland cells of digestive diverticula. | u.a.d. | = Upper anterior dilator muscle. |
| gr.c. | = Granular cells of digestive diverticula. | | |
| i.p.g. | = Internal posterior gastric muscle. | | |

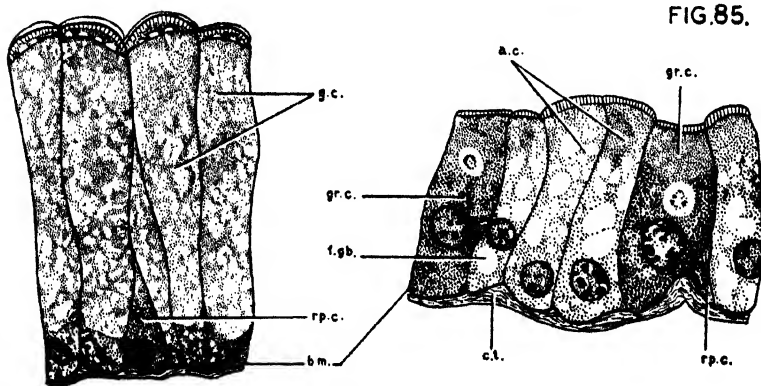
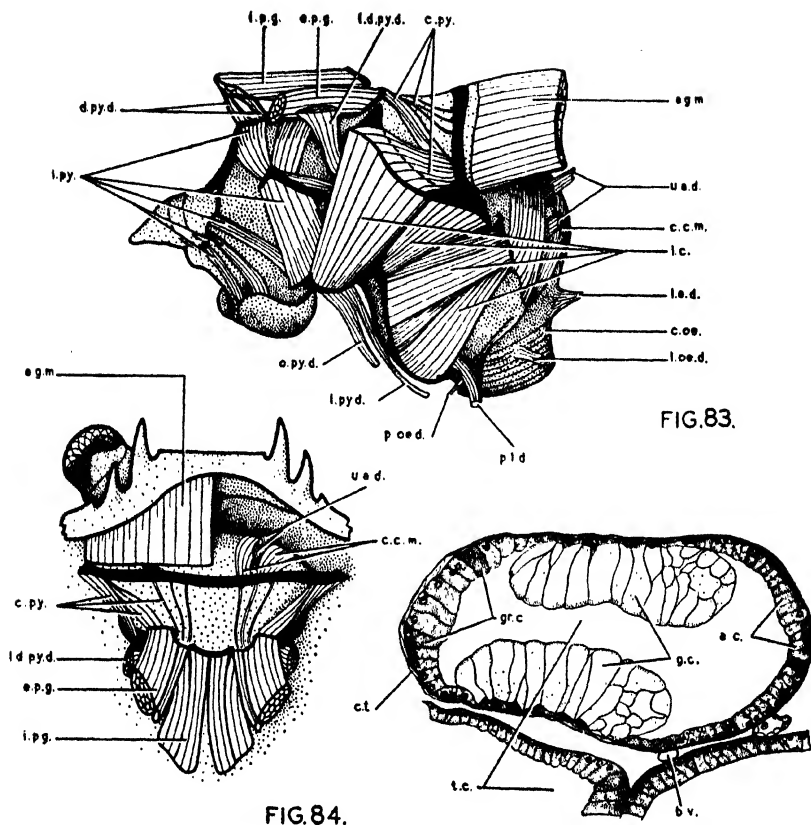


FIG. 86.

FIG. 87.

PLATE XIV.

- Fig. 88. Dorsal view of *G. squamifera* showing the bladder divided into anterior (bl.1, bl.2) and posterior lobes (bl.3, bl.4.). The carapace and the right half of the anterior gastric muscles have been removed to show the anterior lobe of the bladder (bl.1). $\times 3.5$.
- Fig. 89. Anterior view of *G. squamifera* to show the antennary gland (a.g.). The gastric mill, bladder and adductor muscle of the mandibles have been removed. $\times 3.5$.
- Fig. 90. Antennary gland of *G. squamifera* after injection with indigo carmine, showing the reticulation of the labyrinth (lab.). $\times 12$.
- Fig. 91. Antennary gland of *G. squamifera* after injection with ammonium carminate to show the ramifications of the end sac (e.s.). The renal artery (r.a.) is also shown entering the hilum (hil.). $\times 12$.
- Fig. 92. Terminal lobe of the antennary gland of *G. squamifera* showing the end sac (e.s. black) lying in the axis of the lobe and surrounded by the labyrinth. $\times 10$.
- Fig. 93. Transverse section through the antennary gland of *G. squamifera* showing the end sac (e.s.) between the upper (lab.u.) and lower (lab.l.) layers of labyrinth. The relationship of the ureter (ur.) bladder (bl.) and vesicle canal (ves.c.) is shown. The ureter and bladder have turned over to the left during fixation. $\times 35$.
- Fig. 94. Transverse section through lobe of antennary gland of *G. squamifera* showing the types of cell found in the end sac (e.s.) and labyrinth (lab.u., lab.l.). The end sac cells (e.s.) show injected ammonium carminate particles (black). Lying in the lumen of both end sac and labyrinth are desquamated cells (c.c.). $\times 200$.

LETTERING

| | | | |
|--------|------------------------------|--------|--------------------------------|
| a.g. | = Antennary gland. | lab.u. | = Upper layer of labyrinth. |
| a.g.m. | = Anterior gastric muscles. | lab.l. | = Lower layer of labyrinth. |
| apoph. | = Apophysis of mandibles. | oes. | = Oesophagus. |
| bl. | = Bladder. | p.g.m. | = Posterior gastric muscle. |
| bl.1. | = Anterior lobe of bladder. | ps.c. | = Pseudostratified epithelium. |
| bl.2. | = Dorsal lobe of bladder. | r.a. | = Renal artery. |
| bl.3. | = Lateral lobe of bladder. | r.n. | = Resting nucleus. |
| bl.4. | = Posterior lobe of bladder. | st.br. | = Striated border. |
| c.c. | = Cast cells. | ur. | = Ureter. |
| c.v. | = Clear vesicle. | v.c. | = Cell vacuole. |
| e.s. | = End sac. | ves.c. | = Vesicle canal. |
| hil. | = Hilum. | | |
| lab. | = Labyrinth. | | |

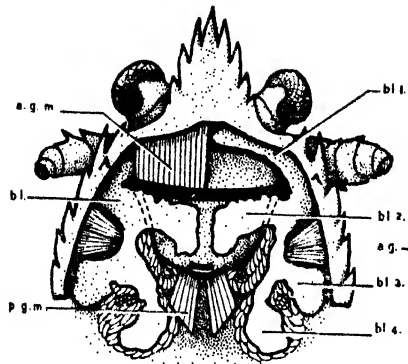


FIG. 88.

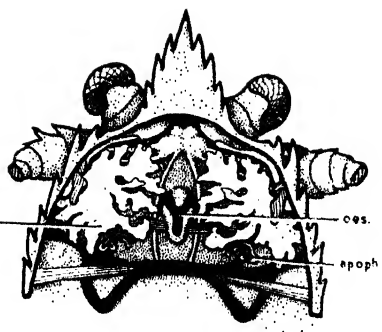


FIG. 89.

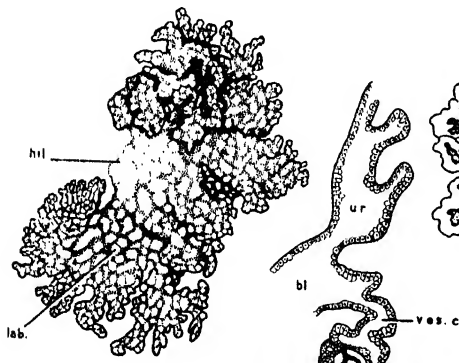


FIG. 90.

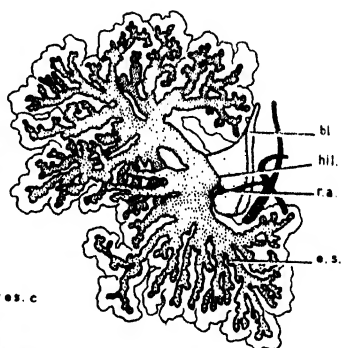


FIG. 91.



FIG. 92.

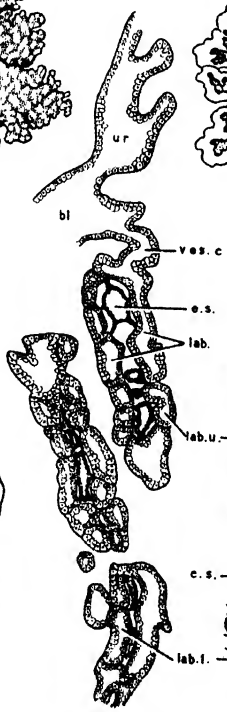


FIG. 93.

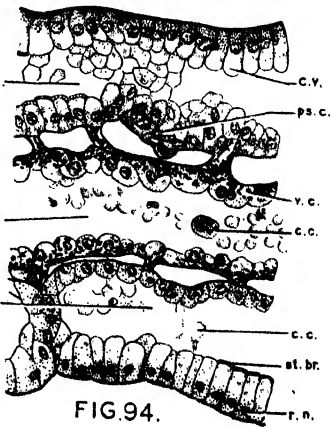


FIG. 94.

PLATE XV.

- Fig. 95. Arterial system of *G. squamifera* lateral dissection. Alimentary tract intact. Remaining organs removed. Numbers refer to appendages, see Plate I, Fig. 2. $\times 3.5$.
- Fig. 96. Arterial system of *G. squamifera* dorsal dissection. Right anterior side has digestive diverticula removed to show hepatic artery (h.a.) and the gastric branch of the antennary artery. On the left side digestive diverticula and bladder are *in situ*, showing the dorsal superficial vessels to these organs from the antennary artery (a.a.). In the abdomen the right side shows the dorsal branches passing over the extensor muscle to supply the dorsal surface of the hind-gut and the lateral branches passing round the flexor muscles to the pleopods. $\times 3.5$.
- Fig. 97. Arterial system of *G. squamifera* ventral dissection. The dissection is carried anteriorly as far as the first maxillipede. The ventral thoracic artery (v.th.a.) overlies the ventral nervous system. In the abdomen the ventral abdominal artery (v.a.a.) gives off branches which pass round the ventral nerve chain to supply the under side of the hind-gut. $\times 3.5$.

LETTERING

| | | | |
|--------|----------------------------|---------|---------------------------------|
| a.a. | = Antennary artery. | p.l.a. | = Posterior lateral artery. |
| bl. | = Bladder. | s.a. | = Sternal artery. |
| d.a.a. | = Dorsal abdominal artery. | t.b. | = Thoracic endophragmal bridge. |
| h.a. | = Hepatic artery. | v.a.a. | = Ventral abdominal artery. |
| h.t. | = Heart. | v.th.a. | = Ventral thoracic artery. |
| l.d.a. | = Latero-dorsal artery. | | |
| m.c.a. | = Median cephalic artery. | | |

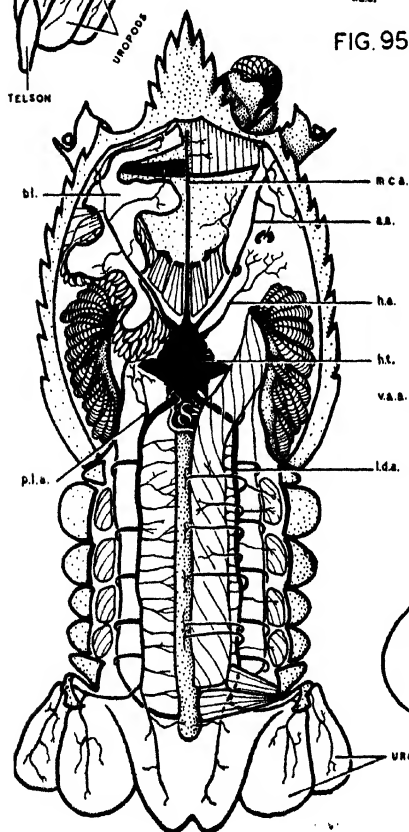
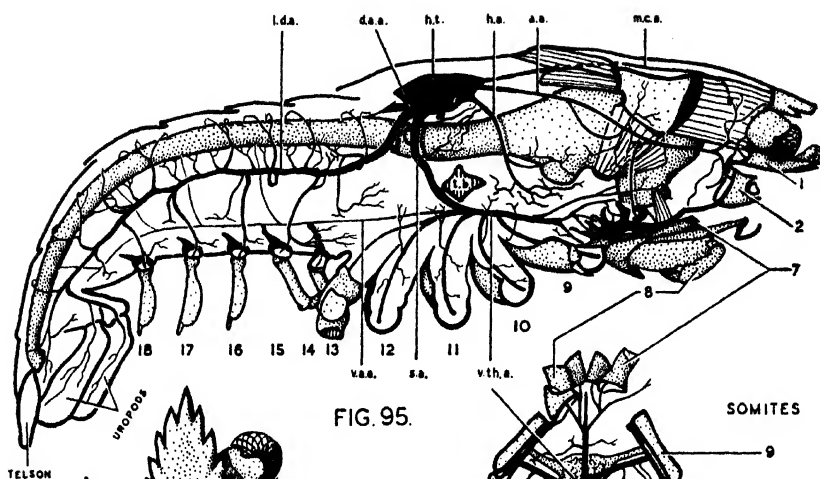


FIG. 96.

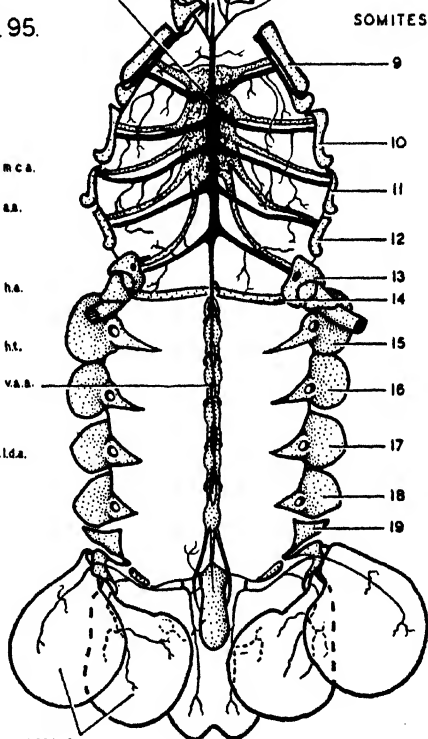


FIG. 97.

PLATE XVI.

- Fig. 98. Section through the antennary artery of *G. squamifera*. This shows the arterial valve (a.v.) which prevents a return blood flow into the heart. Arrow indicates direction of blood flow. $\times 150$.
- Fig. 99. Section through the ostium and heart of *G. squamifera*. The section is to one side of the ostial diameter to show the oblique muscles (o.m.h.) which on systole pull the valve towards the heart cavity thus closing the lips. Arrow indicates the direction of blood flow. $\times 125$.
- Fig. 100. Lateral view of efferent branchial channels of *G. squamifera*. The cut ends show the positions of the phyllobranchiate gills. The numbers refer to the five pereopods. $\times 6$.
- Fig. 101. T.S. through marginal area of gill filament of *G. squamifera* showing the swollen marginal canal. Nephrocyte cells are seen suspended in the marginal canal by the reticular network (ret.n.). The pillar junction cells (p.j.c.) of the lamella shown passing from one side to the other of lamella. $\times 500$.
- Fig. 102. Marginal view of gill lamella of *G. squamifera* showing apparent channels radiating out from the pillar junction cell nuclei. $\times 1600$.
- Fig. 103. T.S. through gill lamella of *G. squamifera* showing pillar junction cells (p.j.c.) divided by transverse septa, and apparent channels through the exocuticle (c.ex.c.). $\times 1000$.
- Fig. 104. A diagrammatic T.S. through thoracic region of *G. squamifera*, showing the blood sinuses and blood channels to the pericardium. $\times 2$.

LETTERING

| | | | |
|---------|--------------------------------|--------|----------------------------|
| a.b.c. | = Afferent branchial channel. | ex.c. | = Exocuticle. |
| a.v. | = Arterial valve. | n. | = Nephrocyte. |
| c.ex.c. | = Channels through exocuticle. | n.s. | = Sphere in nephrocyte. |
| e.b.c. | = Efferent branchial Channel. | o.m.h. | = Oblique muscle of heart. |
| e.c. | = Epithelial cells. | p.j.c. | = Pillar junction cells. |
| epi. | = Epipodite. | pr.c. | = Pericardial cavity. |
| | | ret.n. | = Reticular network. |
| | | v.s. | = Ventral Sinus. |

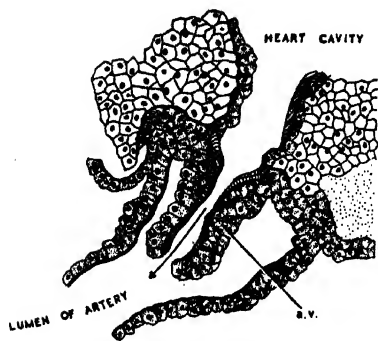


FIG. 98.

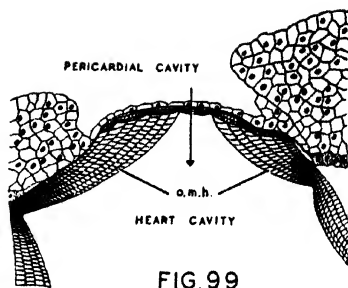


FIG. 99.

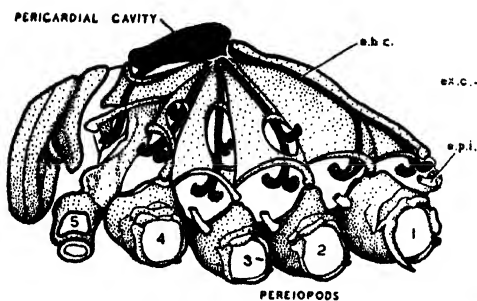


FIG. 100.

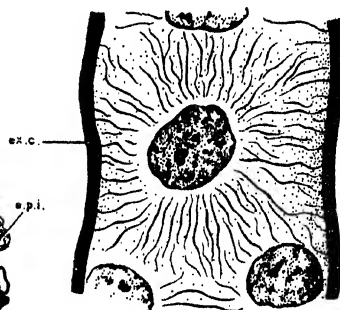


FIG. 102.

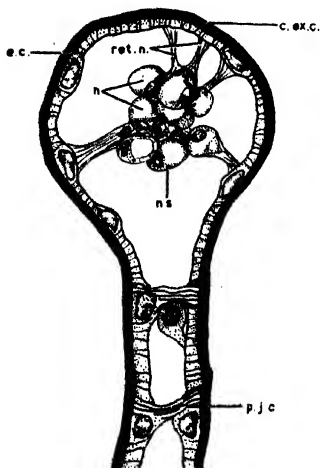


FIG. 101.

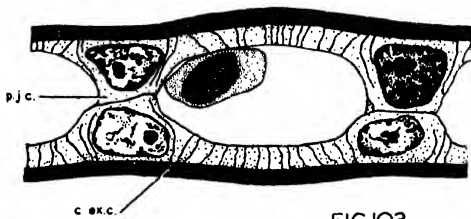


FIG. 103.

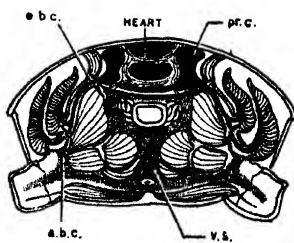


FIG. 104.

PLATE XVII.

- Fig. 105. Nervous system of *G. squamifera* from the ventral side. Nearly all the appendages have been removed.
× 3.
- Fig. 106. Nervous system of *G. squamifera* from the dorsal side. The thoracic endophragmal bridge (t.b.) is shown traversing the main thoracic ganglionic mass. The last two thoracic nerves innervating the abdomen, thread under and over the superficial ventral muscles. × 2.5.
- Fig. 107. Lateral view of the fore-gut of *Galathea squamifera* showing the stomatogastric nerve (s.n.) and its connection with the par-oesophageal ganglion (p.g.).
× 7.

LETTERING

| | | | |
|--------|--------------------------------|-------|--------------------------------------|
| a.g.m. | = Anterior gastric muscle. | rl.n. | = Nerve to rostrum. |
| a.n. | = Nerve to antennule. | s.g. | = Stomatogastric ganglion. |
| ant.n. | = Nerve to antenna. | s.n. | = Stomatogastric nerve. |
| e.n. | = Nerve to eye. | sb.g. | = Sub-oesophageal ganglionic mass. |
| f.a.g. | = First abdominal ganglion. | sp.g. | = Supra-oesophageal ganglionic mass. |
| p.c. | = Post-oesophageal commissure. | t.b. | = Thoracic endophragmal bridge. |
| p.g. | = Par-oesophageal ganglion. | t.n. | = Tegumental nerve. |

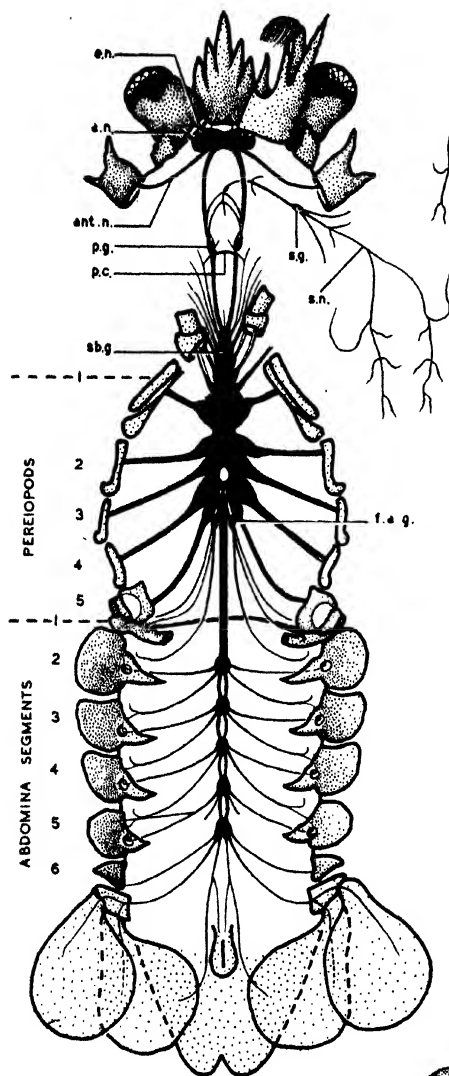


FIG. 105.

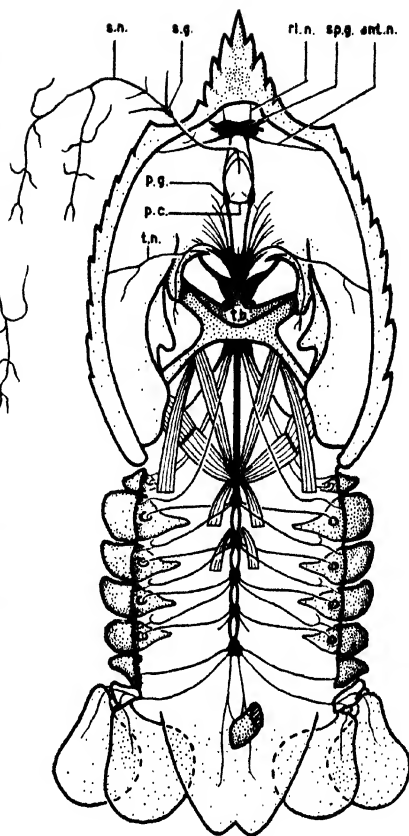


FIG. 106.

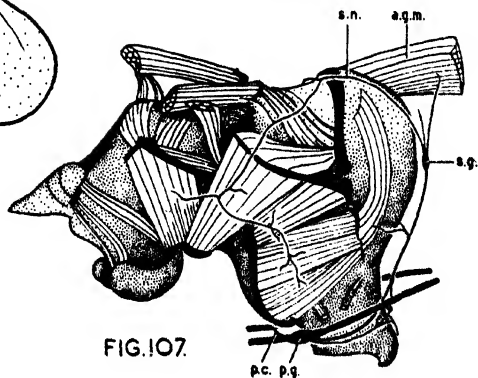


FIG. 107.

PLATE XVIII.

- Fig. 108. Longitudinal section through the eye of *G. squamifera*, showing the situation of the optic centres, the sinus gland and the X-organ. $\times 33$.
- Fig. 109. Longitudinal section through two ommatidia of *G. squamifera*. The ommatidia have sprung apart slightly during section cutting. The letters on the left (A-E) refer to the position of the transverse sections in Fig. 110. $\times 400$.
- Fig. 110. Transverse section through the ommatidia of *G. squamifera*. The positions taken for the sections A-E are indicated in Fig. 109. $\times 250$.
- Fig. 111. Longitudinal section through the sinus gland of *G. squamifera*. The section is not median and so the connection between the inner sinus (i.s.) and outer sinus (o.s.) through the gland is not shown. The dark inner lining of the gland is the structureless membrane. The nerve connection with the medulla terminalis (m.t.) is not shown. $\times 200$.
- Fig. 112. Longitudinal section through the X-organ of *G. squamifera*. Above the X-organ is a portion of the medulla terminalis to which the X-organ is connected by a stout nerve. $\times 200$.

LETTERING

| | | | |
|--------|---------------------------------|---------|--|
| a.p.c. | = Accessory pigment cell. | m.t. | = Medulla terminalis. |
| b.m. | = Basal membrane. | o.s. | = Outer sinus. |
| cn.c. | = Corneagen cell. | p.l.c. | = Pedunculus lobi optici (optic nerve). |
| co. | = Cone. | p.p.c. | = Proximal pigment cell. |
| co.c. | = Cone cell. | p.r.c. | = Proximal retinular cell. |
| cu.f. | = Cuticular facet. | rh. | = Rhabdome. |
| d.r.c. | = Distal retinular cell. | s.gl. | = Sinus gland. |
| i.s. | = Dorso-lateral inner sinus. | s.gl.i. | = Offshoot of the sinus gland. |
| l.g. | = Lamina ganglionaris. | x. | = X-organ. |
| m.e. | = Medulla externa. | | |
| m.i. | = Medulla interna. | | |

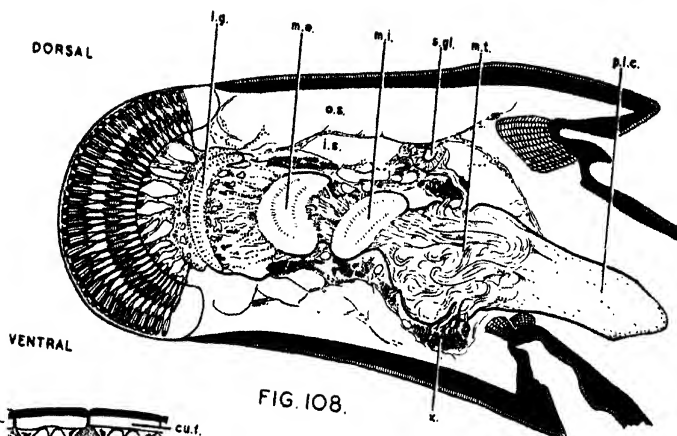


FIG. 108.

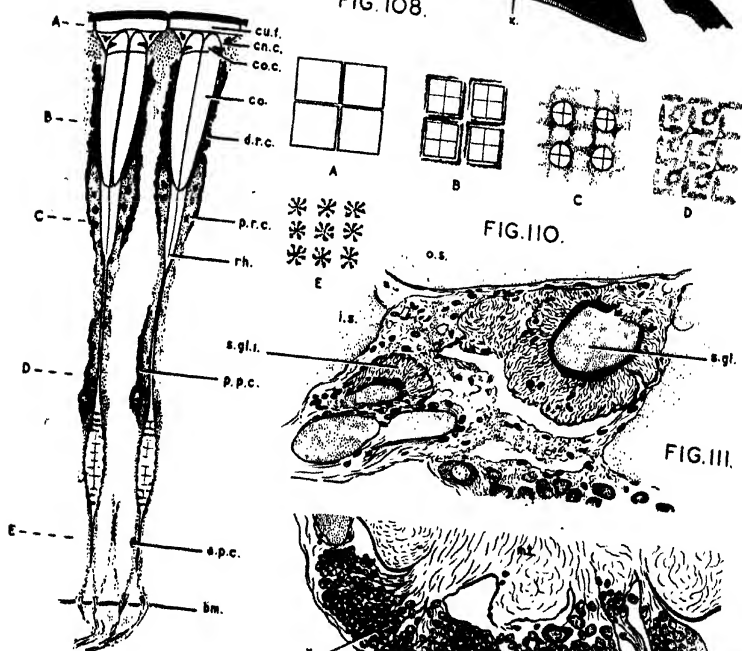


FIG. 109.

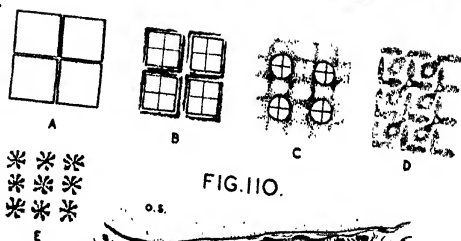


FIG. 110.

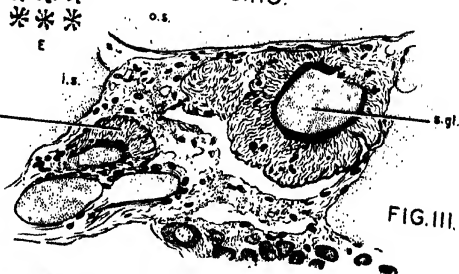


FIG. 111.

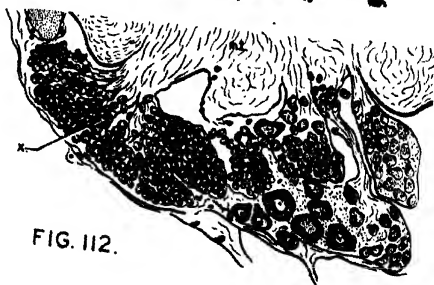


FIG. 112.

PLATE XIX.

- Fig. 113. Left statocyst of *G. squamifera* seen from the ventral side. The extent of the invagination of the keel is shown by the broken line. $\times 23$.
- Fig. 114. Left statocyst of *G. squamifera* seen from the dorsal side. $\times 23$.
- Fig. 115. a. Plumose seta ; b. Non-plumose seta from within the statocyst of *G. squamifera*. Sand grain statoliths are attached only to the plumose setae. $\times 125$.
- Fig. 116. The two distal joints of the antennule of *G. squamifera*. Showing the olfactory spindle (olf.sp.) situated partly within the outer flagellum and partly within the distal end of the third joint. $\times 20$.
- Fig. 117. Longitudinal section through the outer flagellum of *G. squamifera* showing the olfactory nerve (olf.n.) to the spindle (olf.sp.) and the terminal nerve strands (term.s.) from the spindle to the olfactory setae. $\times 40$.

LETTERING

| | | | |
|---------|-----------------------------|-------------|---------------------------|
| k.1. | = Invaginated keel. | s.s.1. | = Simple statocyst setae— |
| k.2. | = Smaller invaginated keel. | position 1. | |
| olf.n. | = Olfactory nerve. | s.s.2. | = Simple statocyst setae— |
| olf.s. | = Olfactory setae. | position 2. | |
| olf.sp. | = Olfactory spindle. | stat.s. | = Statolith setae. |
| | | term.st. | = Terminal nerve strands. |

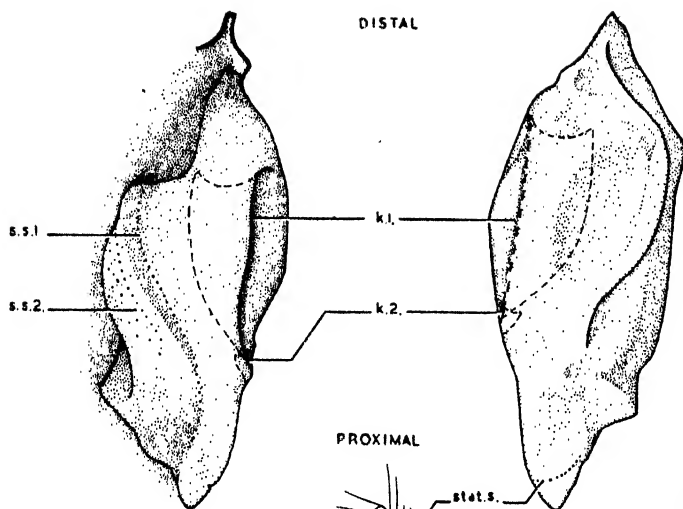


FIG.113.

FIG.114.

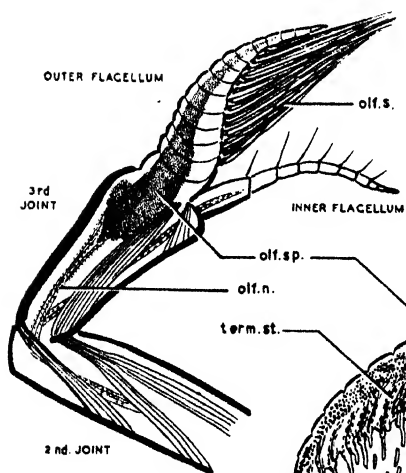


FIG.116.

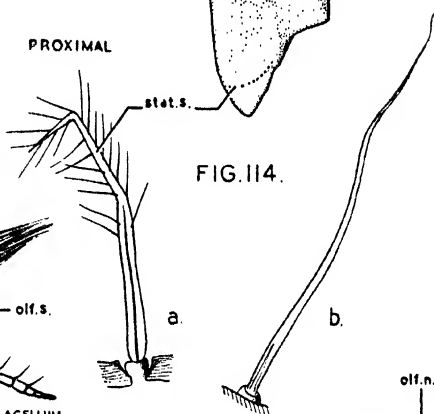


FIG.115.

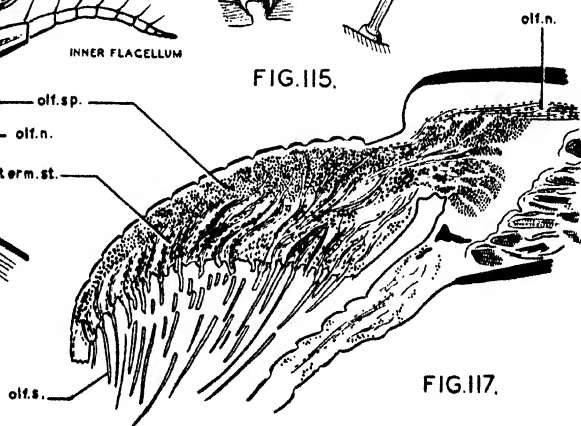


FIG.117.

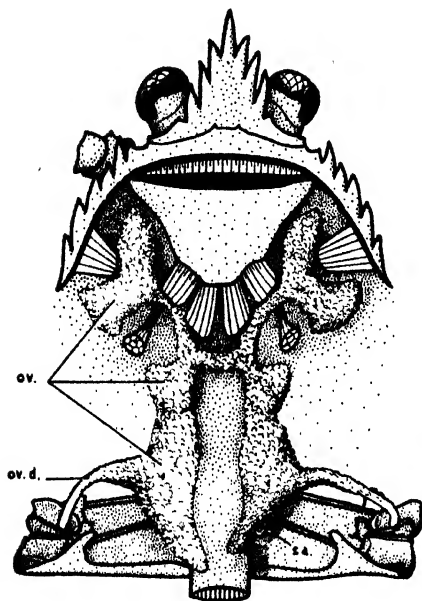
PLATE XX.

- Fig. 118. Female reproductive system of *G. squamifera* from the dorsal side. The oviducts open on the coxae of the third pereopods. $\times 5$.
- Fig. 119. Male reproductive system of *G. squamifera* from the dorsal side. The vas deferens opens on the coxa of the fifth pereopod. $\times 5$.
- Fig. 120. Transverse sections through the vas deferens of *G. squamifera*. $\times 280$.
 A.B.C. Anterior narrow portion.
 D. Posterior wide portion.
- Fig. 121. Single spermatophore of *G. squamifera* attached to a seta of the female pleopod. $\times 660$.
- Fig. 122. Spermatozoan of *G. squamifera*. $\times 1750$.

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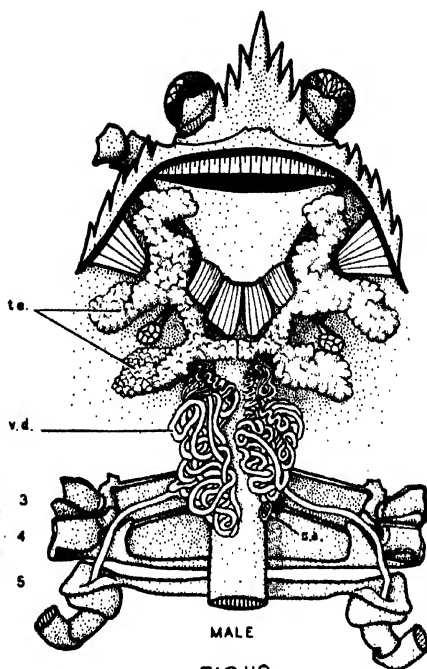
cap. = Capsule of sperm.
 d.c. = Dorsal cells of vas
 deferens.
 grn.l. = Granular layer.
 lat.c. = Lateral cells of vas
 deferens.
 mus.l. = Muscular layer.

nu. = Nucleus.
 ov. = Ovary.
 ov.d. = Oviduct.
 s.a. = Sternal artery.
 te. = Testis.
 vent.c. = Ventral cells.
 v.d. = Vas deferens.



FEMALE

FIG. 118.



MALE

FIG. 119.

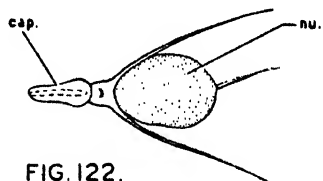
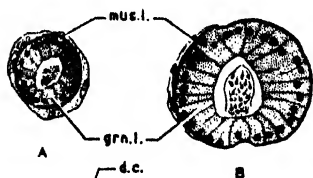


FIG. 122.

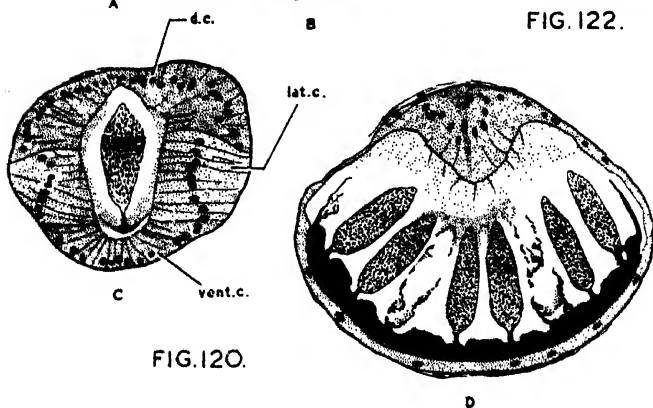


FIG. 120.



FIG. 121.

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